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VOLUME 8 MAY 1939 No. 1

THE FLOOD FACTOR IN THE ECOLOGY OF CAVES

BY R. S. HAWES

From the Zoology Department, King's College, University of London

EXCEPT, perhaps, for the depths of the sea, the large subterranean cave is usually supposed to be the least changeable of all animal habitats, its consistently monotonous factors including a low and almost constant temperature, an atmosphere continuously saturated with water vapour, and permanent darkness. Such an introduction is a commonplace of the textbooks, and, on the whole, what it says is true. The caves of the Istrian and Dinaric karst[1] certainly provide a good many illustrations of the conventional account. For example, Kenk & Seliškar (1931) found the maximum and minimum temperatures of water well inside Podpeška jama to be 9·7 and 9·05° C. over two years: the consistently high humidity is shown by the prevalence of Tettigoniidae such as *Dolichopoda* spp. which can live only in this damp atmosphere (Chopard, 1932): and, of course, the caves are dark.

Clearly, however, the constant effect of these factors may be greatly weakened by the operation of any seasonal variable affecting the animal community. The purpose of these field notes is to draw attention to seasonal variation in caves caused by flooding, a regular feature of the area described. Flooding occurs rather suddenly, so that there is a sharp distinction between conditions in winter, when the caves are under water, and in summer, when they are merely damp. The results include the imposition on the animals of a biological rhythm—a phenomenon contrary to all that we expect of the "constant" cave environment. In addition, floods may operate as agents of distribution; they help in maintaining a regular food supply to caves; and, as mechanical agents, they introduce species from above ground and so initiate colonization.

Popovopolje, in Herzegowina, lies parallel with the Adriatic Sea. It is a typical "polje",[2] about 50 km. long and from 2 to 7 km. wide. In summer, the fertile floor is cultivated. It is surrounded on both sides by dry, barren limestone hills, renowned for their caves. The caves investigated all lie within

[1] Much of Jugo-Slavia consists of the Cretaceous limestone formation called karst, i.e. a barren, rather desolate, countryside, in summer very dry, riddled with caves and with more permanent water below than above ground.

[2] According to J. Cjivić, early in the history of karst formation, surface drainage gave rise to wide, shallow river canyons. When the soil became porous, the drainage became subterannean, and the abandoned river bed is the polje of the present day. Low lying and damp, the verdant polje contrasts strongly with the surrounding barren country of the typical karst.

about 8 km. of the village of Zavala and hold some of the most remarkable and highly specialized, as well as the rarest, of cavicolous species. Vjetrenica pećina, for example, the largest cave in south-eastern Europe, is the home of the blind prawn, *Troglocaris*, the blind Mysid, *Troglomysis* (Stammer, 1933), and of the giant white Amphipods, *Niphargus* (=*Stygodytes*) *balcanicus* and *Metohia carinata* (Absolon, 1927). The cavicolous Urodele Amphibian, *Proteus anguineus*, although rare, also occurs as far south as this.

At all times of the year there is, in some of the caves, a good deal of water, and some, too, are connected by permanent and well-defined underground rivers. Typically, in summer, the walls and floors are damp, except where pools or lakes occur. But in winter, after heavy rains, the underground rivers swell, and pour out of the caves to flood the polje; the mouths of the caves opening at the margins of the polje are themselves submerged, so that, when the waters turn back, whirlpools are created. The peasants at these times cross their own maize fields by boat. Obviously, this violent periodic disturbance must have important ecological effects, and these are most likely to be surprising within the caves, because, in other respects, the cave environment tends to be constant. I have grouped the kinds of effects obtained under three headings. The examples are chosen because they are fairly easy to study, and are suitable for discussion in an introductory sketch of this sort.

(1) *The annual rhythm.* This unexpected and interesting effect may be illustrated by a cave, known as Crnulja, not far from Turković. This is one of the very few known habitats of the Serpulid polychaete worm, *Marifugia cavatica* (Absolon and Hrabě, 1930), which is to be found, in places, in such dense profusion that walls, ceiling and floor are completely covered by huge masses of the tiny, calcareous tubes. For most of the year, the tubes are out of water, the worms withdrawn and covered by a thin film of water of condensation. As is well known, the Serpulidae are characteristically marine animals and very few indeed (e.g. *Mercierella* in Europe) are known outside the sea. It is therefore somewhat astonishing to find a fresh-water Serpulid confined to a cave and living most of its life out of water. How the creature feeds during the dry months is completely unknown.

In the same cave occur a Plumatellid, noted by Remy (1937), who found it in August 1936 in a desiccated condition and stuffed with statoblasts, and a sponge, *Ephydatia mülleri* Lieberkühn, whose gemmules I discovered among the worm tubes a year later. The ordinary sponge gemmule germinates in spring, stimulated probably by a rise in temperature: this stimulus can be used to induce germination artificially at any time of the year (Brien, 1932). But the cavicolous strain must germinate in winter, the only time when the flood water is available, and it is highly probable that this water is colder than the air in which the gemmules have been lying. I was able to show that gemmules from Crnulja do not respond to temperatures which stimulate epigean forms (Hawes, 1938), and it seems reasonable to relate this reversal of the

temperature reaction to the demands on the animal made by periodic flooding. There are thus three fresh-water species belonging to predominantly marine groups characterized by free-swimming ciliated larvae, so that sexual reproduction must be confined to the wet months. Alternate drought and flood impose on these organisms a regular alternation of quiescent and active phases.

(2) *The food problem.* Since caves are dark and animals ultimately depend for their food on green plants, all cavicolous food chains must include some link with the outside world. The colonies of coprophagous beetles living on bat dung in the cave are a good example (Jeannel, 1926). The retreat of the flood waters through caves from the open polje is another such link, and probably the most useful importation here is wood. Nearly all the caves contained some wood, often in great quantity, very rotten and covered with fungi. It was noticeable that pieces of wood were centres of attraction for many animals, especially Collembola, also Thysanura and Isopoda (particularly *Titanethes* spp.) and occasionally Phalangida and Pseudoscorpionida.

Though floods introduce food into caves, the final supply to aquatic animals is not insured. After the recession of the floods, a population previously distributed throughout a relatively large volume of water may be confined to numbers of shallow and more or less isolated pools for as long as eight or nine months. If the pools are close together, as they often are, Amphipods such as *Niphargus* may wriggle from one to another, so that isolation is imperfect. The Entomostraca of the mud bottoms no doubt contribute importantly to the economy of the pool population. But some observed cases evade these suggestions. One pool, about 2 by 1 m. and 6 cm. deep, contained a score each of the large and active Crustacea, *Troglocaris* and *Niphargus balcanicus*. These animals were quite isolated and must have been at least eight months out of reach of an external food supply.

(3) *Colonization.* We may consider flooding (*a*) as a means of passively transferring already cavicolous animals from one cave to another and (*b*) as effecting initial colonization of a cave by previously epigean species. There is no need to dwell on the mechanism by which an animal may be washed out of one and into another cave, but the second point calls for more attention.

How animals came to be in caves at all has been the subject of much conjecture. The following account of the habits of *Paraphoxinus* indicates one approach to the problem.[1] This small Cyprinid fish is, apart from one Spanish species, confined to the Balkans. It is most commonly found in caves, but where there exists a permanent communication between subterranean and surface waters it often occurs in the latter all the year round. Elsewhere, the fish spend most of their time underground, but the floods wash them out in such great quantities and so regularly that the peasants know when and

[1] I am indebted to Dr E. Trewavas for some help with cave fish, but it does not necessarily follow that she lends her authority to my opinions. For a general account of *Paraphoxinus*, see Spandl (1926).

where to look for them and have designed a special method for collecting the catch. Breeding occurs at this time, and the young fish are left to pass a year in the open, though their parents are carried back into the caves. (Possibly the eggs are laid in protected, shallow water, and there they stay, while the older, active fish get involved in the main stream of receding water.) After the next flood, the young fish in turn are swept into the caves. The question is—Are we dealing with a cave dweller which is occasionally washed into the open, or with an essentially epigean fish which is having a cavicolous habit forced upon it? The latter seems to me to be nearer the truth. *Paraphoxinus* occurs above the ground at all times of the year when the opportunity exists. Where it lives mainly in caves it does so because, for most of the year, the only available water is underground. It breeds above ground, and it seems to be unaffected by a change of environment which would act disadvantageously on a more typical cavicolous form thus extracted from its peculiar home.

Is there any evidence that the compulsory adoption of a cavicolous environment is having any effect on *Paraphoxinus*? Its eyes are normal; the suggestion that they are rudimentary (Apfelbeck, 1895) is quite without foundation. But the fish exhibits one character, a tendency to reduced scales, which is remarkably common among cave fishes in general. The reason for this character seems not to be understood—possibly it has to do with increased sensitivity of the skin—but it is certainly very prevalent. Cave fishes are commonly derived from families in which the scales are reduced or absent, e.g. catfish, or the Brotulids of Cuba. Or, if they are members of scaly families, they may independently reduce or lose their scales, e.g. *Barbus* has large scales but, of its cavicolous derivatives, *Caecobarbus* has somewhat reduced scales and *Phraeactichthys* has lost them entirely (Norman, 1926). The genus *Paraphoxinus* is distinguished by the reduction of its scales from the related *Phoxinella*. Are we not justified, then, in concluding that we are here watching the early stages of the colonization of caves by an epigean fish, already beginning to show a typical cavicolous character, and that the responsible agent is flooding?

Summary

1. Although our conception of the persistent constancy of the cave environment may be confirmed again and again by measurements of temperature, humidity and light, the conception is upset by a study of flooding.

2. In a fairly small area of Herzegowina it was found that there was a regular alternation of summer drought and winter flood.

3. This alternation may impose on the animals living in the affected caves a recurrent cycle, in which a quiescent and an active phase regularly succeed each other.

4. Merely as a mechanical agent, flooding plays an important part in maintaining the food supply to caves; within the caves, the recession of the

waters may create special food problems by isolating animals for long periods in small pools.

5. By carrying animals from one to another cave, flooding accounts for certain facts of local distribution. An example is given to show how flooding may act as the cause of initial colonization of a cave by an originally epigean species of fish.

Acknowledgements

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THE DISTRIBUTION OF WILD DEER IN ENGLAND AND WALES

By WILLIAM LING TAYLOR

Observation extending over the past twenty-five years forces the conclusion that in many parts of the country the population of deer at large in a wild state was considerably greater and more widespread in the early years of the present century than was generally recognized. Evidence has since been accumulating that numbers are tending to increase. Forest Officers in charge of the lands acquired by the Forestry Commission in England and Wales since the passing of the Forestry Act, 1919, which now extend to 568,700 acres, have had exceptional opportunities of noting the distribution of the various species of wild deer and their density on the ground. Inspections covering many thousands of acres of privately owned woodlands confirm the experience recorded and there are few of the more densely wooded districts in which deer of one kind or another are not present.

The species native to Great Britain are the red deer (*Cervus elaphus*) and the roe deer (*Capreolus capreolus*). The status of the fallow deer (*Dama dama*) is not so clear, but it has unquestionably been resident in England for a long period, chiefly within the confines of deer parks, but at large elsewhere, as in New Forest and in the Forest of Dean until 1874, from times concerning which no precise information is available. Other species have been introduced into parks and enclosures in more recent years. Individual specimens of these have escaped from time to time and have established themselves as breeding species in those parts of the country in which the escapes have occurred and from which the deer have spread and found sanctuary. Japanese deer (*Sika nippon*), the Chinese muntjac or barking deer (*Muntiacus reevesi*) and the Siberian roe (*Capreolus pygargus*) have been added to the wild fauna of Britain. All three, particularly the Japanese deer, are tending to increase their range and numbers. The Siberian roe and the Chinese muntjac appear at present to be the most strictly localized of the introduced species. It is possible that other exotic deer are at large in small numbers, but none is recorded as having acclimatized itself in or about the newly formed forests or the older Crown Woods.

Deer are woodland animals and conditions to the south of the Scottish border appear to suit them well. The truly indigenous red deer (*Cervus elaphus*) has never been exterminated from West Somerset and Devon where it is still numerous. Wild red deer also occur on the eastern side of the Lake District of Cumberland, Westmorland and North Lancashire, in the New Forest and in a semi-wild state in Savernake Forest in Wiltshire. Where they are to be found at large in other parts of England and Wales they appear to be the

progeny of escapes from enclosed private herds. The wild red deer has survived because of its value for hunting and stalking, and its continuation in its remaining strongholds is due to the considerable degree of protection that has been extended to the species. In its true woodland habitat the red deer is a magnificent and conspicuous animal and if all protection were withdrawn its final suppression in England and Wales could only be a matter of time.

The roe-deer (*Capreolus capreolus*), which is the most truly feral in its habits of all our wild deer, occurs in Northumberland, Cumberland and the Lake District at least as far south as Morecambe Bay. It is established also in the eastern midlands and more strongly in the south of England, particularly in Dorset, Hampshire, Surrey and Sussex. It is numerous in East Anglia in the neighbourhood of Thetford and Brandon as a result of an introduction of some forty or more years ago.

The range of the roe is enlarging both in the north, south and east and, as it breeds freely and is small and well equipped to take care of itself, it is increasing its numbers and in some localities is multiplying with considerable rapidity. It is unquestionable that the afforestation of large areas is aiding this species and, on occasion, numbers have here and there to be reduced; but it is also without question that the roe, which can maintain itself in the face of enclosure and agricultural development without artificial aid, is likely to continue to do so all the more with the additional shelter afforded by the recent afforestations. A very little consideration of the circumstances in which this animal has survived will clearly indicate that of the larger members of the British fauna none is more secure from extinction under existing circumstances than the roe-deer.

The position of the fallow deer (*Dama dama*) is different. The stock from which the fallow deer now at large about the countryside have been drawn is chiefly escaped animals from the herds in the deer parks that still remain as part of the demesnes of many private estates. Possible exceptions occur in New Forest where wild fallow deer are still plentiful, and where record of the origin of the stock has been lost, and on Cannock Chase in Staffordshire. The herd of fallow deer in Savernake Forest and neighbourhood is doubtless also of ancient origin. The fallow deer in the Forest of Dean in Gloucestershire have completely disappeared in that area. An Act of 1668 (20 Carolus II, cap. 8) provides that for the prevention of destruction to young wood by overcharging the Forest with deer not more than 800 deer of all sorts may be kept in the Forest at any one time. In 1849 it is known that there were about 400 deer left, but by 1874 the old stock of fallow deer had all gone. There remains no local recollection of deer of other species than fallow and no deer of any kind are now left in the Forest of Dean, but there is a small herd of fallow deer in the adjacent Highmeadow Woods. Fallow deer running wild occur in large or small numbers in many other districts, notably, as regards numbers, on the Welsh borders of Herefordshire and South Shropshire, in

Nottinghamshire, in parts of Kent, Surrey and Sussex and in Wiltshire and Hampshire. Speaking generally, this species is the most widely and evenly distributed of all wild deer in England and Wales.

The Japanese deer (*Sika nippon*) has established itself in east Dorset and in the New Forest. It is also reported from east Kent and is probably to be found elsewhere. The Chinese muntjac (*Muntiacus reevesi*) is making its way into the woodlands of Bedfordshire and Northamptonshire. The Siberian roe (*Capreolus pygargus*) also occurs at large in the same parts of the country.

Deer in Great Britain have few, if any, natural enemies. Foxes may take a few of the calves and fawns on occasion, but for the rest almost the only dangers come from man. Where deer are plentiful, they are a source of loss to the farmer and to the forester and in excessive numbers are unlikely to be tolerated. Recently wild deer have been suspected as carriers of foot-and-mouth disease and some efforts to suppress them have resulted. In moderate numbers they do little harm and can be an interesting addition to the amenities of the countryside, also, as in the case of the red deer, an attraction to the sportsman. Numbers, however, are not always easy to control. The Deer Destruction Act of 1851 (14 and 15 Vict. c. 76), which applied to the New Forest, resulted in a determined effort to exterminate the deer in that area but the effort proved abortive and there are probably almost as many red, fallow and roe deer in the New Forest to-day as ever there were; the deer population of the New Forest has also been augmented by the more recent invasion of Japanese deer from east Dorset. In those parts of the country which are already populated by deer these animals may quite easily become a problem, for inevitably someone must pay for their keep, either directly or indirectly, and in some localities they are already a nuisance to husbandry.

The following list has been compiled from reports of observations made by the Forestry Commissioners' Officers in England and Wales over the period extending from the passing of the Forestry Act, 1919 to 1938. It does not purport to be an exhaustive record of the present distribution of the various species of wild deer, but it gives an indication of the widely spread areas over which deer occur, and of their relative local abundance:

County	Forest area	Species	Density
Northumberland	Kielder	Roe	Numerous
	Redesdale	,,	Not numerous
	Harwood	,,	Numerous
	Rothbury	,,	,,
	,,	Fallow	Not numerous
Cumberland	Kershope	Roe	,,
Durham	Chopwell	,,	,,
	,,	Fallow	Occasional
	Hamsterley	,,	,,
Lancashire	Grizedale	Red	Numerous
(Furness)	,,	Roe	,,
Yorkshire	Allerston	Fallow	Occasional
Nottinghamshire	Clipstone	,,	Numerous
Lincolnshire	Bourne	,,	Not numerous
	Kirby Underwood	,,	,,

County	Forest area	Species	Density
Staffordshire	Cannock	Fallow	Numerous
Shropshire	Mortimer	,,	,,
Worcestershire	Wyre	,,	,,
Herefordshire	Haugh	,,	,,
Northamptonshire	Hazelborough	Siberian roe	Not numerous
	Salcey	,,	,,
	Fineshade	Fallow	,,
	Fermyn	,,	Numerous
	Yardley	,,	,,
	,,	Siberian roe	Not numerous
Rutland	Pickworth	Roe	Numerous
Norfolk	Thetford	,,	,,
	Harling	Fallow	Not numerous
Suffolk	Brandon	Roe	Numerous
	Mildenhall	,,	,,
	King's Forest (Culford)	,,	,,
	Rendlesham	Fallow	Not numerous
Bedfordshire	Ampthill	Chinese muntjac	,,
	,,	Siberian roe	,,
Gloucestershire	Highmeadow	Fallow	,,
Kent	Hemsted	Unidentified	,,
	Challock	Fallow	Numerous
	,,	Japanese	,,
Sussex	Buriton	Unidentified (more than one species)	Not numerous
	Goodwood	Roe	,,
	,,	Fallow	,,
	Marden	,,	Numerous
Surrey	Chiddingfold	Roe	,,
Hampshire	New Forest	Red	,,
	,,	Roe	,,
	,,	Fallow	,,
	,,	Japanese	,,
	Ringwood	Roe	Not numerous
	,,	Fallow	Occasional
	Alice Holt	,,	Not numerous
	Bramshill	,,	,,
Wiltshire	Gardiner	Roe	,,
	Westwoods	Fallow[1]	,,
Dorset	Puddletown	Roe	Numerous
	Wareham	,,	Not numerous
	,,	Fallow	Occasional
	,,	Japanese	Not numerous
Somerset	Quantocks	Red	Numerous
	Bruton	Fallow	Occasional
Devon	Brendon	Red	Numerous
	Dartmoor	,,	Occasional
	Eggesford	,,	,,
	Okehampton	,,	,,
	Haldon	,,	Not numerous
	Halwill	Fallow	,,
	Lydford	Red	Occasional
Cornwall	Bodmin	,,	Not numerous
	,,	Fallow	Occasional
Caernarvon	Gwydyr	Roe	,,
Merioneth	Coed-y-Brenin (Dolgelley)	Fallow (?)	,,
	Cynwyd	Unidentified	,,
Montgomery	Kerry	Fallow	,,
Carmarthen	Brechfa	Unidentified	,,

[1] Red deer also reported.

THE HABITAT, DISTRIBUTION AND DISPERSAL OF THE PSYCHID MOTH, *LUFFIA FERCHAULTELLA*, IN ENGLAND AND WALES

By RICHARD S. McDONOGH

(*With* 3 *Figures in the Text*)

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1. Introduction

This paper is part of the results of a biological investigation of the small Psychid moth *Luffia ferchaultella* (Stephens). The species is parthenogenetic and wingless. The larvae are case-bearers and live on tree trunks and sometimes on stones (e.g. at Stonehenge), feeding on lichens of the genus *Lecanora* (Fig. 1*a–d*).

The investigation was carried out at the Biological Field Station of the Imperial College of Science and Technology, Slough, Buckinghamshire, under the direction of Prof. J. W. Munro. I wish to thank Dr O. W. Richards, lecturer in entomology at the Imperial College, for suggesting the work, and for his invaluable assistance and great interest throughout.

2. HABITAT

(*a*) *Local distribution*

(1) *Lichen.*

Luffia ferchaultella is only found in situations having a sufficient supply of its lichen food, in particular *Lecanora*. This lichen contains the green alga *Pleurococcus*. This alga is very widespread and occurs on most tree trunks, fences, and walls in the country. It is not very common in town areas.

There are two types of green growth commonly present on tree trunks. There is a bright green form, usually damp-looking, which is composed of *Pleurococcus* only: besides this there is a darker green variety which looks drier than the previous type. This is a lichen since it is a mixture of green alga and fungal hyphae. It is certainly a *Lecanora*, probably *L. varia*, which is the commonest species of the genus. Identification of the lichen requires the reproductive bodies of the fungus. Various stages of the colonization of the *Pleurococcus* by the fungus are often present on the tree, the two forms, lichen and alga, merging into one another. *Lecanora varia* is a very primitive form of lichen, often hardly reaching the condition of a true lichen.

The moth larvae eat the *Pleurococcus* growth to some extent; but where, as often happens, both this and the lichen are on the same tree, the number of larvae present seems to be dependent on the area covered by the lichen (see Tables 1–3).

On a series of 6 in. squares on some horse chestnuts at Slough the following numbers of larvae were found.

Table 1

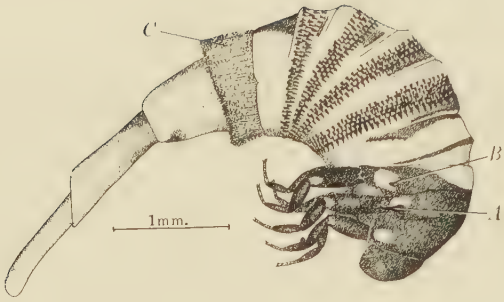
	Squares with *Lecanora* present	Squares with both types present	Squares with *Pleurococcus* present
Total no. of larvae in six squares	21	2	0
Average no. per square	3·5	0·3	0

A continuous belt 6 in. wide at varying heights round a similar horse chestnut was divided into types and the larvae counted:

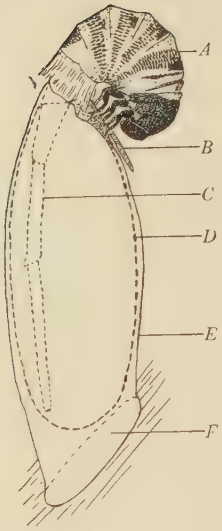
Table 2

	Lecanora present	Both types present	*Pleurococcus* present	Height of belt (ft.)
No. of larvae	6	2	0	5
,,	9	3	0	4
,,	7	2	0	3

A more detailed count of larvae on the two types of green growth is tabulated in Table 3. It is based on a 6 in. wide area round a horse chestnut at a height of 4 ft. 6 in. above ground-level.



a



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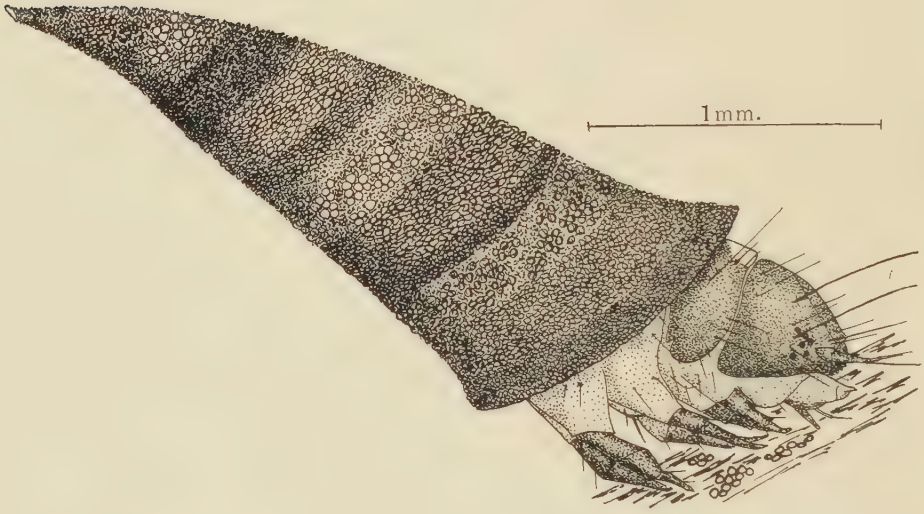

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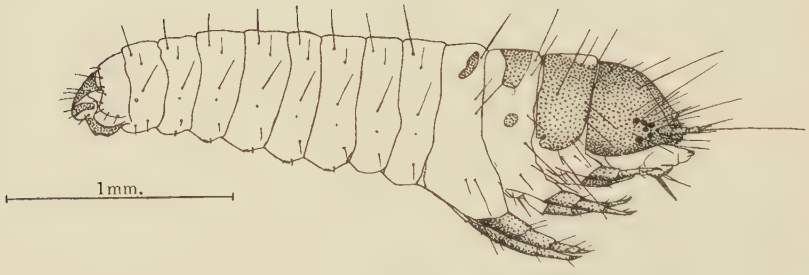

d

Fig. 1.

Table 3

	Length of band in.	No. of larvae Nov.	No. of larvae April	Total larvae	No. per in.
60% *Lecanora* thick growth	5	11	14	25	2·5
80% *Lecanora* patchy growth	2·5	5	6	11	2·2
90% *Lecanora* thick growth	5	28	25	53	5·3
No *Lecanora*	3	1	2	3	0·5
No *Pleurococcus*	1·5	2	1	3	1·0
80% *Pleurococcus* thick growth	6	1	0	1	0·08
Both types present but scattered	6	2	4	6	0·5
Both types present thick	6	3	4	7	0·6

It will be seen that the 12·5 in. of the band which had more than 60% *Lecanora* had the majority of the larvae. Eighty-nine larvae were on this *Lecanora*, six on the bare areas, thirteen on the mixed areas, and one on the *Pleurococcus*. The lengths of these areas were 12·5, 4·5, 12 and 6 in. respectively: the average number of larvae per inch of circumference being 7·12, 1·33, 0·5 and 0·15.

(2) *Species of tree.*

The species of tree appears to have little influence, provided the lichen is present. Trees with a deeply creviced bark tend to support a larger number of larvae than do those with a smooth bark. There are one or two exceptions to this generalization. Horse chestnuts, which usually have a smooth bark, are often well stocked with larvae. This is probably due to the heavy growth of lichen (usually *Lecanora varia*) which these trees often possess. Furthermore, the tree occurs commonly in the type of country favoured by *Luffia*, i.e. open park land type. Elms are very rarely well stocked with the moth, though they possess deeply creviced bark. This is probably due to the predominance of *Pleurococcus* only on them where a green growth occurs, though elm bark is not commonly covered by any green growth at all. A hard white lichen is very common on elms, but this does not appear to suit *Luffia ferchaultella* and *Lecanora* is rare. When the moth occurs on stones it apparently feeds on lichens other than *Lecanora varia*, though probably of the same or closely allied genus.

A census of trees near Slough likely to have the moth on their trunk (i.e. in open country) was done. The figures given in Table 4 represent approximate percentages of the different species having the larvae present in four degrees of abundance, estimated by general impressions.

Legend to Fig. 1 a–d.

Fig. 1*a*. Adult. *A*, forewing (reduced to small thoracic flap). *B*, hind wing. *C*, fringe of long scales forming an anal tuft (used by the adult to block the upper aperture of the case after oviposition in the pupa case).

Fig. 1*b*. Diagram showing oviposition. *A*, adult female. *B*, facemask of pupa case (displaced by adult on emergence). *C*, ovipositor inside pupa case. *D*, position of pupa case. *E*, algae or bark-covered larval case. *F*, spun-down mouth of larval case (larva turns round, faces the apex of the case before pupating).

Fig. 1*c*. Almost full grown larva as it appears on the tree.

Fig. 1*d*. Almost full grown larva without case.

Table 4. *Percentage of trees with larvae present in different densities*

Species	No. of trees examined	Abundance of larvae (%) None	Few	Fair no.	Numerous
Willows (*Salix*)	34	10	40	47	3
Oak (*Quercus*)	238	15	20	61	12
Horse chestnut (*Aesculus hippocastanum*)	105	25	13	26	12
Beech (*Fagus sylvatica*)	38	39	17	26	8
Elm (*Ulmus*)	175	50	28	22	0
Birch (*Betula*)	26	54	27	19	0

Willows are the most likely to have some larvae on them. The low number of willows having large numbers of larvae on them is probably due to these not usually possessing thick growths of *Lecanora*. The second best tree is oak, which has been used in this investigation to map the distribution of the moth. It is the tree most likely to be present in all localities, and to have the larvae, if the moth occurs in that place. Probably the commonest tree in this country is elm, but it is of little value for estimating the distribution of *Luffia* since a large proportion are without larvae. Though their bark is not very creviced, both beech and horse chestnut are often well inhabited, since many of them have very heavy growths of lichen, particularly when they are growing in the type of situation favoured by *Luffia ferchaultella*. Birch has the larvae on its bark when the smooth white areas have become broken. On old birch trees fairly large (though seldom *very* large) colonies of the moth have been found.

Some other trees have been observed with the moth on them. Ash (*Fraxinus elatior*) is often heavily infected. It is comparable to the oak in this respect, but it is a much less common tree and was therefore of less value in this survey. Lime (*Tilia*), apple (*Pyrus*) and plum trees (*Prunus*) are often well stocked with the moth, but the prevalence of the lime in urban areas, where lichens do not thrive, causes *Luffia* to be less common on them than on similar trees in rural districts. The same applies to planes (*Platanus acerifolia*) and sycamores (*Acer pseudoplatanus*). The moth has also been found on hornbeam (*Carpinus betulus*), rowan (*Pyrus aucuparia*), lilac (*Syringa*), locust (*Robinia pseudoacacia*), sweet chestnut (*Castania sativa*), alder (*Alnus glutinosa*), hawthorn (*Crataegus*), holly (*Ilex aquifolium*), *Laburnum*, black poplar (*Populus nigra*), Lombardy poplar (*P. italica*) and white poplar (*P. alba*). As a rule gymnosperms do not have enough lichen on them to support the moth. A few larvae have been found on silver fir (*Abies alba*), but no pupated cases were seen. Austrian pine (*Pinus nigra austriaca*), cedar (*Cedrus libanotica*), Scots pine (*Pinus sylvestris*) and yew (*Taxus baccata*) have not yielded more than a few larvae, though numerous trees have been examined.

(3) *Position of tree.*

The position of the tree is an important factor. The larvae are not found on trees in a wood if the tree is more than 20 yards from the edge, unless the

undergrowth is very thin. Trees surrounded by thick bushes do not have the moth on them. This effect is well illustrated by a group of trees studied at Epping. The result of the shading bushes is indicated in Fig. 2.

Besides this screening effect due to trees and undergrowth there is another caused by sudden rises in the ground-level. A group of trees situated on the top of a hill will more often than not be uninfested by the moth, though the trees are apparently suitable. This phenomenon has been observed in several localities, notably near Chingford in Essex, at Harrow, and also near Barnet. Small but abrupt hills have a similar effect to that caused by large hill masses, e.g. on the Chilterns (see p. 20), though the reasons for this are probably different. Gentle undulations do not affect the distribution. The optimum type of country for the moth is open park land such as Richmond Park or Windsor Great Park, where there are plenty of trees situated in unscreened positions.

Fig. 2. Diagram map of a group of trees near Chingford. The circles represent the positions of the trees in a small area of Epping Forest near Chingford. The shaded areas *A*, *B* and *C* are groups of undergrowth, chiefly thick hawthorn. The space south of the trees is open country for over a mile. *D* is a large store hut. The only trees with an open prospect to the S.W. are 1 and 2. They alone have large numbers of moth larvae on them. 3 and 10 which are about 15 yards in from the edge of the forest have some larvae on them but not many. 4–7 and 11–15, though all well covered with *Lecanora*, are without larvae. 8 and 9 are also shaded and also lack the moth, but had very little alga on their trunks. This suggests that trees having a fairly open prospect, especially to the S.W., the weather side, tend to have more larvae on them than do trees which are protected from the wind.

(4) *Age of tree and its isolation.*

It has been found that a tree is unlikely to be inhabited by the moth before it has attained a circumference of 6–8 in. A permanent colony is not usually formed until the bark begins to be creviced. It is probable that the larvae can be carried on to trees from distances of over $1\frac{1}{2}$ miles (p. 24).

(*b*) *Distribution of larvae and pupae on the tree*

Except during periodical migration the larvae tend to be more numerous on the lower parts of the trees. There is a south and east orientation, probably due to a light factor, though the prevailing west winds may have some effect.

The density of the larvae per 6 in. square on horse chestnuts at Slough is given in Table 5. The figures for each height are based on counts of about 15 squares from areas covered by *Lecanora*.

Table 5

Height above ground	Average number of larvae per square				
	North	East	South	West	Average for whole circumference
5 ft.	0·5	1·75	3·0	0·75	1·5
4 ft.	1·5	2·0	5·0	0·5	2·25
2 ft.	0·75	2·5	7·5	0·75	3·0
6 in.	3·75	3·75	19·75	3·0	6·25

The averages are given to the nearest 0·25. The counts were made in May.

The final positions of the larvae are indicated by the counts of the spun-down pupated cases made on an apple and a plum at Slough (Table 6).

Table 6

Height in ft. ...	0–1	1–2	2–3	3–4	4–5	5–6	6–7	7–8
			Plum					
No. of pupae	44	84	110	60	36	20	—	—
Pupae per 6 in. sq.	0·5	0·9	1·3	0·7	0·5	0·3	—	—
			Apple					
No. of pupae	69	72	84	36	22	8	14	5
Pupae per 6 in. sq.	0·7	0·8	1·0	0·4	0·3	0·1	0·1	0·04

While the maximum number of larvae appears to be usually very near to the ground, the pupae tend to be higher up the tree. Irregular distribution is commoner on smooth bark than on well-creviced trees. The amount of alga and lichen controls the distribution of the larvae, but the pupae tend to be more affected by the distribution of cracks in the bark which act as places for pupation. There seems to be a tendency for the south and east sides of a tree to have the majority of the pupae (Table 7).

Table 7

Height on tree (ft.)	Number of pupae per quadrant				
	North	East	South	West	Total no.
0–3	11	32	27	9	79
3–5	12	14	14	2	42
0–5 Total	23	46	41	11	

(*c*) *Effect of light intensity*

A series of experiments was carried out to discover the light limit below which the larvae would not live. That such a limit existed was suggested by the distribution of the larvae on the lower and better illuminated parts of the

trunk. The intensity of illumination was measured by decomposition of oxalic acid solution by light under the catalytic action of uranyl sulphate exposed in Monax test-tubes (Atkins & Poole, 1929). The method adopted measured the mean horizontal illumination over the period when the tubes were exposed. The light values for any position were obtained in terms of a fraction of the total light present in the open during the time of measurement. The tubes were exposed for periods of 2 hr. at midday between 12 noon and 2 p.m. during May, June and July. This was the period when the larvae were most active and the trees were in leaf. Control tubes were exposed in the open, and two or three were also kept in the dark to act as zero controls.

A set of green screens was made to cover part of a tree trunk, so that the light intensity over that part of the surface was reduced. They were in three degrees of density and are referred to here as light, mid- and dark green screens. At the beginning of each experiment a known number of active larvae was placed under each of the screens. After 24 hr. the position of the larvae under the screens was noted. Two areas 4 and 6 in. square were marked under the centre of each screen. The number of larvae found in the squares was taken as a measure of the effect of the screens on the movement of the larvae compared with the movement of a similar set of larvae in a control area without the screens. The total of five such experiments using about 20 larvae each per screen is shown in Table 8.

Table 8

Screen type	No. larvae started	No. larvae found	No. found in 4 in. sq.	No. found in 6 in. sq.
Control	100	56	15	33
Dark green	104	86	6	34
Mid-green	99	63	17	37
Light green	112	85	31	55

Table 9 shows the figures expressed as percentages of the numbers found after each experiment.

Table 9

Light intensity (full light in open = 1·0)	Screen type	% in 4 in. sq.	% in 6 in. sq.
0·117	Control	26·8	56·2
0·023	Dark green	7·4	37·2
0·047	Mid-green	31·8	56·2
0·070	Light green	37·8	60·4

The number of larvae present on a tree becomes very small at a height of about 8 ft. (These results were obtained on a series of chestnuts at Slough: the figures obtained may not necessarily hold at other localities.) At the highest point at which larvae are found the light intensity was about 0·025 of that in the open. This amount of illumination was found at various heights on the trees studied at Slough; but usually it was about 7–8 ft. up the trunk and nearly always coincided with the usual upper limit of the larvae. Larvae were

found higher but only in small numbers compared with the number present on the lower portions of the trunk. It will be noted from Table 9 that the dark green screen was much more effective than the other two in causing the larvae to leave the squares under them, and that it was this one which cut down the light below the normal intensity limit of the larvae as measured on the trees. It is therefore very probable that the moth larvae will not as a rule live in nor move into areas of the tree where the light intensity is less than 0·025 of the light in the open.

The light intensities measured at various heights on the trees are illustrated by the following example:

Height (ft.)	1·0	1·5	3·5	4·5	7·0	8·5	10·0	12·0
Intensity	0·236	0·278	0·179	0·118	0·052	0·047	0·014	0·019

The greater intensity about 1–2 ft. from the ground was noted in several experiments. It is probably due to reflection from the ground. The large numbers of pupae found in this area of the trunk may be correlated with this fact. The effect of light colour upon larval movement is referred to later in the paper.

3. Distribution in England

The records of *Luffia ferchaultella* given by Tutt (1900) are not very numerous. He mentions twelve localities: four from Sussex, three from Surrey, two from Kent, and one each from Essex, Gloucestershire and Herefordshire. A study of all the available county faunal lists added a little to these records, but the number of known localities was surprisingly small, considering the abundance of the species in the south of England. On suitable trees it is often very numerous. More than 400 specimens have been collected from one tree in a locality where it was previously unrecorded. The main distribution of the species in this country has been fairly well determined during this investigation (Fig. 3).

A suitable tree, usually an oak or chestnut with adequate growth of *Lecanora*, was examined in each locality. If larval cases of *Luffia ferchaultella* were found on it, the locality was noted on the map with a spot. If no cases were found on the trees examined, the absence of the species was assumed and the locality was marked with a cross. The negative records are not to be regarded as absolute. In most localities they are based on an examination of five to ten trees which were suitable for the larvae, and would therefore be expected to have them if the species occurred in that part of the country. It can be safely assumed that where there are negative records the species, if it was present, was so in numbers far below normal.

The moth has been found to occur over the whole of south England with the exception of Cornwall. Its western limit in the south appears to be the eastern edge of Dartmoor and Exmoor. It has not been found in Wales. The

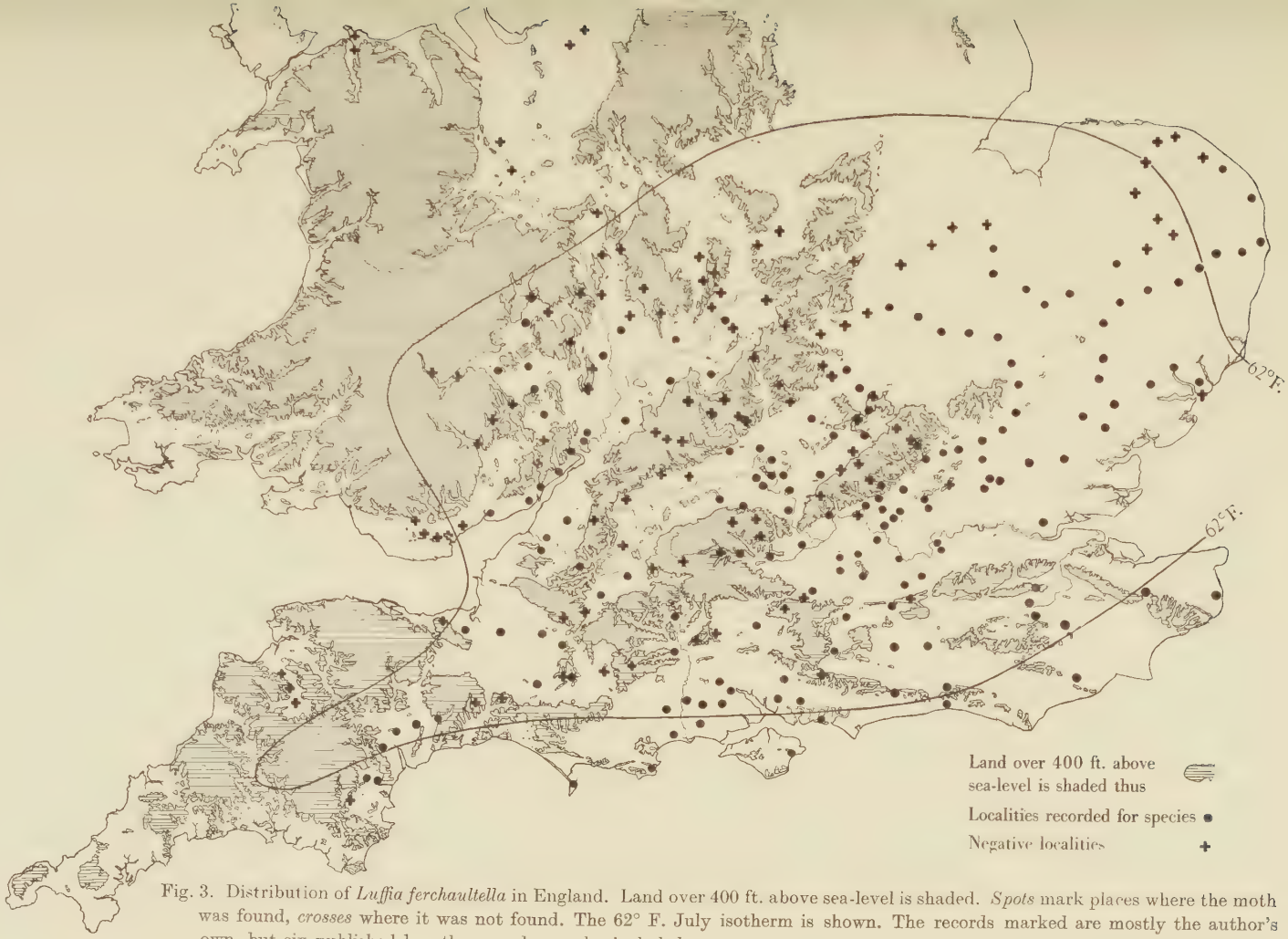

Fig. 3. Distribution of *Luffia ferchaultella* in England. Land over 400 ft. above sea-level is shaded. *Spots* mark places where the moth was found, *crosses* where it was not found. The 62° F. July isotherm is shown. The records marked are mostly the author's own, but six published by other people are also included.

western limit here seems to be near a line from Newport, Monmouth, up to Leominster. The latter is the most northerly point in the west of England where the moth has been found. It is present over the lower Severn Valley as far as Droitwich, and up the Avon to just above Warwick. The species is present over most of East Anglia. Its northerly limit appears to follow a curved course from Northampton via Kettering, March, Downham Market, Swaffham, to a few miles north of Thetford. From Thetford the limit apparently turns north and reaches the east coast near North Walsham in Norfolk.

Over this range it has been observed that the moth keeps to the valleys and is rarely found at a greater height than 400 ft. above sea-level. Both the Chiltern and Cotswold ridges produce a definite break in the distribution of the species. In the northern and eastern parts of its range it appears that the height limit becomes lower. This is particularly shown over the East Anglian Ridge and in Norfolk. It is also indicated by the distribution of the moth on the higher ground between Thames and Ouse Valleys. Near the Northampton uplands the moth becomes scarce and is absent some distance below the 400 ft. contour line. The moth is quite scarce in the Avon Valley above Warwick, and it dies out entirely below Coventry, well below the 400 ft. level. In the Severn Valley, the Clent Hills and south Shropshire Hills form a barrier to the species, which does not occur as far north as Kidderminster, though this town is much below 400 ft. above sea-level. It is present sporadically, often quite common, over the plain of Hereford, but I have found it nowhere at places over 350 ft. above sea-level.

In the upper parts of the Thames and Bristol Avon Valleys, between Lechlade and Bath, the moth seems to be very scarce, though here again the land is under 400 ft. South of the Thames it has been found over the 400 ft. line, but usually the downs have so few trees that the moth is quite uncommon. Where suitable trees occur on the higher parts the moth may be found, but it is very irregularly distributed in such places. There is an area in the New Forest district where the moth is present but uncommon. This is probably because either thick woods or open heathland occur over most of this country, and neither type of country suits the species.

The species is very common over the whole middle Thames Valley, and in the district immediately round Oxford. It is also numerous in the north of Essex. In the lower Thames area, both north and south of the river, the moth is much less common. Over the Metropolitan area it is unknown, though it occurs commonly in suitable habitats on the outskirts of Greater London.

With the exceptions noted the moth covers the rest of its range fairly evenly; in the east, where there are no hills to act as barriers the moth dies out gradually. Near the limits pupated individuals become rare, though during the early part of the moth's life-history period, late summer and autumn, large numbers of larvae can be found. These fail to survive the winter and do not pupate. A similar effect has been observed in the valleys on the south slope of

the Chilterns. As the valley ascends the number of old pupated cases gets less, though the trees examined may have numbers of early instar larvae. At the scarp slope of this ridge the density of the species increases much more rapidly. There is very little shadow effect. The same population gradient has been observed on the Cotswold Ridge.

The species covers a range nearly completely enclosed by the 62° F. (16·4° C.) isotherm for July, the month when the adults emerge and oviposit. The areas where the range overlaps the isotherm are localities with a high sunshine record for the same month. The excess hours of sunshine might be expected to make up for the slightly lower average temperature. The northern limit of the species seems to be rather far south of the 62° F. July isotherm. This could be explained by the effect of average annual temperatures on the larval stages, since apparently it is they which fail to survive the winter in the areas near the northern limit.

The records for *Luffia ferchaultella* are arranged under counties. Except for the localities marked with an asterisk, the records were obtained personally. Most of them are new county records. The moth had not been recorded previously from Bedfordshire, Cambridgeshire, Devon, Huntingdonshire, Middlesex, Monmouthshire, Norfolk, Northamptonshire, Somerset, Suffolk, Warwickshire, or Worcestershire.

The following abbreviations are used:

c. common. f.c. fairly common. v.c. very common. v.f. very few. r. rare. Names in brackets, e.g. (Tutt), after localities marked with an asterisk refer to its source.

BEDFORDSHIRE: Leighton Buzzard f.c. BERKSHIRE: Abingdon c.; Ascot f.c.; Hungerford c.; Jealotts Hill f.c.; Marpledurham c.; Newbury f.c.; Stanford in the Vale f.c.; Theale v.c.; Wallingford f.c.; Wantage f.c.; Windsor Great Park f.c.; Wokingham c.: Bagley Wood* (Microlepidoptera of Oxford District, 1928[1]); Cothill* (Microlep. Oxf. Dist. 1928); Kennington* (Microlep. Oxf. Dist. 1928); Tubney Wood* (Microlep. Oxf. Dist. 1928). BUCKINGHAMSHIRE: Amersham v.f.; Aylesbury f.c.; Beaconsfield f.c.; Bourne End f.c.; Burnham Beeches c.; Fenny Stratford f.c.; Iver c.; Langley c.; Slough c.; Rickmansworth f.c.; Waddesdon f.c.; Winter Hill (Marlow) not c.; Wolverton f.c. CAMBRIDGESHIRE: Cambridge f.c.; Caxton Gibbet not c.; Chatteris c.; Ely f.c.; Fordham not c.; March not c.; Stump Cross f.c. DEVONSHIRE: Alphington f.c.; Clyst Honiton c.; Chudleigh not c.; Honiton f.c.; Kingsteighton c. DORSETSHIRE: Sherborne f.c.; Portland* (Tutt); Purbeck* (Tutt). ESSEX: Chelmsford v.c.; Chigwell v.c.; Colchester v.c.; Earls Colne v.c.; Epping c.; Orsett not c.; Ongar c.; Stansted few; Waltham Abbey f.c.; Wendon f.c.; Witham v.c.; Bowers-Gifford* (Tutt). GLOUCESTERSHIRE: Chaxhill c.; Cheltenham f.c.; Gloucester c.; Iron Acton; Lydney c.; Newnham

[1] **Waters, E. G. R. (1929).** "A list of the micro-lepidoptera of the Oxford district." Rep. Ashmol. Nat. Hist. Soc. 1928: 1–72.

c.; Bristol* (Tutt). HAMPSHIRE: Cadnam f.c.; Cosham not c.; Frimley f.c.; Greatham not c.; Iford few; Ibsley f.c.; Lyndhurst not c.; Picket Post f.c.; Ringwood f.c.; Sleaford c.; Shedfield f.c.; Sutton Scotney f.c.; Titchfield f.c.; Totton f.c.; Wilverleyn Post f.c.; Yateley f.c. HEREFORDSHIRE: Hereford f.c.; Leominster f.c.; Portway f.c.; Ross-on-Wye f.c.; Tarrington* (Tutt). HERTFORDSHIRE: Barnet f.c.; Bishop's Stortford f.c.; Hatfield c.; Leverstock Green f.c.; Redbourn c.; St Albans f.c.; Ware f.c.; Cheshunt* (Tutt). HUNTINGDONSHIRE: Great Staughton f.c.; St Neots c. KENT: Sevenoaks c.; Tonbridge f.c.; Tunbridge Wells c.; Deal* (Tutt); Goudhurst* f.c. (O. W. Richards); Lewisham* (Tutt); Maidstone f.c. MIDDLESEX: Harrow c.; Hatch End f.c.; Laleham v.c.; Northolt f.c.; Uxbridge f.c. MONMOUTHSHIRE: Chepstow f.c.; Llanwepn f.c.; Magor f.c. NORFOLK: Caister r.; Great Ormesby f.c.; Harleston c.; Scole f.c.; Stalham f.c.; Thetford c. NORTHAMPTONSHIRE: Higham Ferrers not v.c. OXFORDSHIRE: Dorchester f.c.; Henley-on-Thames f.c.; Sandford f.c.; Tetsworth f.c.; Witney r.; Woodstock r.; Dorchester*, Oxford* and Yarnton* (Microlep. Oxf. Dist. 1928). SOMERSETSHIRE: Butleigh f.c.; Castle Cary not c.; Corston nr. Bath f.c.; Crewkerne f.c.; Long Ashton c.; Nether Stowey f.c.; Weston f.c.; Woolverton f.c. SUFFOLK: Beccles not v.c.; Bungay f.c.; Bury St Edmund's not c.; Capel c.; Hepworth few; Ipswich f.c.; Ixworth not c.; Long Melton c.; Mildenhall f.c.; Oulton not c.; Sudbury c.; Trimley c.; Wortham c. SURREY: Chertsey f.c.; Dorking not v.c.; Egham c.; Guildford not c.; Oxshott f.c.; Richmond c.; Ripley f.c.; Wimbledon c.; Camberwell* (Tutt); Claremont Park* (Tutt); Peckham (Tutt). SUSSEX: Battle f.c.; Horsham c.; Petworth c.; Steyning c.; Arundel* (Tutt); Hayling* (Tutt); Horsham* (Tutt); Shoreham* (Tutt). WARWICKSHIRE: Alcester f.c.; Shipston-on-Stour not c.; Warwick not c. WILTSHIRE: Seend f.c.; Stonehenge c. (on stones); Stonehenge* (Tutt as *L. lapidella*); Wilton f.c. WORCESTERSHIRE: Droitwich f.c.; Powick c.; Wickhamford f.c.

4. DISPERSAL

(*a*) *From tree to tree*

(1) *Method of dispersal.*

The occurrence of the moth suggests that it is distributed by wind dispersal. Trees which were screened from the wind did not have the moth on them. During the early instars the larvae are easily blown off their trees, especially as they spin long lengths of silk which might act as parachutes (see Tutt, 1900, p. 249) in much the same manner as do the similar structures spun by some young spiders. The older larvae are less easy to blow off, but even they have been observed to be carried away when walking about on windy days. (Jones & Parks (1928) state that the first stage larvae of *Thyridopteryx ephemeraeformis* spin themselves silk parachutes and are by this means carried from one tree to another. This occurs both before and after their bags have been spun. Haseman

(1912) records the infestation of rose-bushes by wind transportation of young larvae over a distance of $\frac{1}{4}$ mile.)

Definite proof that the larvae are blown off their tree by the wind has been obtained. A number of narrow sheets of plywood, covered on one side with a thin layer of adhesive material, were set up round a tree on a cylindrical framework. There were nine boards which were 6 in. wide and 2 ft. 6 in. long arranged equidistant from each other and at a distance of 18 in. from the tree. There was about 12 in. space between each board. The tree was therefore covered for one-third of its circumference, and shielded from the wind to this extent. If any larvae were blown off there would also only be one-third of them caught on the boards. The arrangement covered effectively about 2 vertical feet of the tree at a height of 4 ft. above the ground.

Between 10 November and 10 December two larvae were caught on the boards, having presumably been blown off the tree. Since the adhesive surface was facing the tree they are very likely to have come from the tree. The tree trunk carries larvae for about the first 6 ft. It may be assumed therefore that during this month about 20 larvae may have been blown off the tree. The reverse experiment, of having adhesive surface facing outwards from the tree to catch larvae blown on to it has not been tried.

Both the larvae caught from the tree were third-instar larvae. An old pupated case was also detached and blown on to the boards. Whether older larvae can be easily blown off cannot be decided; the pupated case in question was much less heavy than an old larva would be.

(2) *Rate of colonization.*

A series of dated trees at Burnham Beeches has been used to estimate the speed with which a tree could be infected. All the trees were beeches which are smooth-barked and consequently not the ideal type of tree for the larvae to stay on. One tree planted 3 years previously (in 1932) and about 6 in. in circumference had no larvae. A 4-year-old tree (planted 1931) of the same size had at least one larva. A tree which had been there for 5 years (i.e. since 1930) had a few *Luffia* present, but it was rather less infected with lichen than were the other trees examined. A tree which had been there for 7 years (since 1928) had about 15 larvae on it, the girth of this tree being 15 in. Two older trees, 10 and 16 years old and 17 and 36 in. in circumference respectively, were well infected with the moth. All the trees studied had adequate amounts of the lichen *Lecanora*, and were all more or less well situated, and within 100 yards of each other. The oldest tree, 52 years old and 60 in. in circumference, had few larvae, possibly because of its low branches and very thick foliage -probably a light effect rather than an example of wind screening. The other trees had very few leaves. These results appear to suggest that the moth can reach a tree within 4 years of planting as a sapling. This limit is much too early if the plant is grown from a seedling. In this event the tree is unlikely to be colonized

before it has attained a circumference of 6–8 in. The youngest tree with previous year's cases on it was a 7-year-old specimen having a girth of 15 in. This is about the size at which the bark begins to be creviced.

The same set of trees was examined again in the following year. The 3-year-old tree (now 4 years) which had no larvae on it the previous year now had at least two. The 4-year (1931) tree still had only one larva. The 5-year (1930) tree that had not very much *Lecanora* on it and only a few larvae, now had at least 30 larvae though the amount of lichen was unchanged. A tree planted in 1929 and 15 in. in circumference had one pupal case of a previous year's larva; in 1935 it had no pupated cases.

It can be assumed that a tree may become colonized by the moth within 2 years of attaining a circumference of 6 in. A creviced bark is usually necessary for a permanent colony to develop.

(3) *Distance covered.*

The distance over which the moth can be transported has not been accurately estimated. The larvae have been found on trees isolated by over half a mile from other occupied trees. The larvae on the monoliths of Stonehenge are even farther from the nearest trees, a group of beeches about a mile away. These trees are not themselves colonized, for an intensive search on them failed to reveal a single larva. The nearest occupied tree was approximately $1\frac{1}{2}$ miles away.

The distance over which the larvae can be carried is further indicated by the occurrence in the Chiltern valleys of early instar larvae on trees having no sign of pupal cases. Such temporary groups of larvae have been found up to 5 miles from the nearest known trees with permanent colonies on them.

(*b*) *Migrations on the tree*

It has been observed that massed migrations of the larvae on a tree may occur at times. Several of these migrations were noticed in 1935 before the full-fed larvae spun themselves down for pupation. During the year 1936, however, they were not repeated, at any rate to the same extent. Migration may be only obvious in years when the species is very numerous, as happened in 1935 when the phenomenon was noticed. The larvae moved up the tree in a more or less compact group about a month before pupation. This was noted on four trees at the Slough Biological Field Station, two trees in particular showing it very well. The subsequent behaviour of the larvae on these two trees was observed regularly. The migration which occurred during the summer 1935 is shown by the larval counts given below.

The figures italicized are the higher values noted during each count. Between 24 and 28 May the larvae moved about 3 ft. up the tree and tended to become confined to a narrower band than before. As the total number of

larvae was reduced they appeared to begin to spread again over a wider band. This may, however, be the result of the maxima becoming less distinct.

Table 10. *Migrations of larvae on plum tree*

Date ...	24 May	27 May	28 May	30 May	31 May	1 June	2 June	3 June
Height above ground (ft.)	Numbers of larvae							
0– 1	54	20	17	15	12	5	—	—
1– 2	92	41	28	28	28	17	—	—
2– 3	180	92	38	33	30	13	11	—
3– 4	150	100	30	27	21	10	8	—
4– 5	*580*	130	33	29	24	8	3	—
5– 6	*200*	*180*	28	29	31	12	7	—
6– 7	150	*700*	*997*	*840*	*474*	70	*53*	—
7– 8	70	90	*300*	*250*	*302*	*128*	*27*	—
8 –9	—	15	60	78	90	66	20	—
9–10	—	—	—	9	14	11	—	—
Total no.	1476	1368	1531	1338	1026	340	129	104

During the next year no such migration was detected. The total number of larvae present on the trees was considerably less than in 1935. There was a slight suggestion of an upward move on an apple tree about 3 June but the numbers involved were not large enough to be significant.

(*c*) *Factors affecting the activity of the larvae*

(1) *Temperature and humidity.*

The amount of movement occurring during the year appears to vary as the temperature changes. The humidity has also an effect. In one of his notes on the Psychidae, Chapman (1901) says that *Luffia ferchaultella* larvae hide in cracks during warm weather, presumably to avoid desiccation. He also (erroneously) states that they cannot walk over the lichens in dry weather. Consequently, he says, a wet winter gives them more opportunity to feed and hence to grow larger. It has been observed during this investigation that the larvae are only really active in mild damp conditions. On cold and windy days they are usually to be found in crevices on the trees. The effect of the weather on the species is mentioned by Burrows (1923), who observed periods of scarcity over a period of years which he ascribes to adverse conditions. Bruand (1853) also attributes this periodic scarcity to hard winter months.

During the winter the larvae are certainly less active than in the autumn and early summer. Between the beginning of December and the end of February they feed very little or not at all. During these months there is a corresponding period of cessation of growth. There is a decided increase in the proportion of the larvae which do not move for some time during this period (see Table 11). The movements were traced by putting a coloured pin touching the tip of each larval case and noting any change. Owing to the small size and surface texture of the larval cases, it was impracticable to mark individuals with paint.

Table 11. *Effect of temperature on the movement of larvae on a tree*

Date ...	Sept.–Oct.	Oct.	Oct.–Dec.	Dec.–Feb.	Feb.–Mar.	Mar.–Apr.	Apr.–May	May–June	June–July
Proportion not moved per period	0·002	0·08	0·24	0·42	0·21	0·20	0·17	0·09	0·04
Period in days	27	30	33	26	26	28	30	28	30
Proportion of days below 40° F. (4·4° C.)	0·00	0·00	0·18	0·49	0·50	0·11	0·00	0·00	0·00

During 12 days in the December–February period the temperature was continually below 35° F. (1·7° C.), while there were no days during the February–March period when the temperature failed to rise above this for some time in the day. This difference between the two periods explains why the amount of larval movement is so much less during December and February than in the next period, although the number of days having a temperature maximum below 40° F. is about the same.

The critical temperature for larval movement was estimated by experiments in a form of refrigeration apparatus in which the larvae were inactivated by cooling. The first series of experiments was carried out in March. These indicated that the larvae are inactive at temperatures below 39° F. (4·0° C.). It is possible that feeding does not occur to a great extent below 45° F. (7·0° C.).

Similar experiments were performed in May to ascertain if there was a difference in the critical temperature later in the life history of the species. No significant difference was observed in this temperature though the temperature at which the larvae regained *full* activity after cooling appeared to be 2–3° C. higher. Care was taken to standardize as far as possible the rate of initial cooling of the larvae as this was noted to have some effect on the recovery temperature.

(2) *Light.*

A well-marked positive phototropism was observed in the larvae. A number of larvae were placed under a circular glass cage which was illuminated from one side by a lighted slit. The positions of the larvae after being left for a period were recorded. If they had moved into the lighted quadrant they were considered positive. Those moved into the lateral quadrants were noted as neutral. Various colours of light were used and a summary of some of the experiments is given in Table 12.

It is of interest to note the greater effect recorded by the red light. This would tend to make the larvae migrate *from* areas illuminated by green light, i.e. foliage shaded areas, into parts having more reddish lighting. It has been noted that the larvae do migrate away from green lighted portions of the tree, though this is also caused by the actual intensity of illumination as well as the colour.

Table 12. *Effect of light on larval movement*

Light	Negative	Neutral no. larvae	Positive time	Not moved	Total time min.
White	8	62	572	120	51
Red	0	0	140	0	10
Blue	0	0	72	40	8
Green	10	175	617	205	73
Dark controls	181	116	131	89	32

The movements are given below in the form of average number per minute moving towards the light.

Light	Negative	Neutral	Positive	Not moved
White	0·16	1·22	11·20	2·35
Red	0·00	0·00	14·00	0·00
Blue	0·00	0·00	9·00	5·00
Green	0·14	2·40	8·49	2·81
Dark controls	5·65	3·63	4·10	2·78

(3) *Geotropism.*

The young larvae appeared to exhibit a certain amount of negative geotropism when in captivity. If a few larvae are placed in a tube a thick accumulation of silk on the cork and upper parts of the tube indicates where the larvae have been walking. The lower portions of the tube are usually clean. A similar result is obtained if the tube of larvae is kept in the dark. In their natural habitat this tendency to climb is not obvious except during the migrations noted above. Larvae collected just before pupating and placed in cages with a suitable log of wood on which to spin down also showed a tendency to climb, about a quarter of the larvae finally spinning their case to the muslin cover of the cage and often in the crevice between the top and the rim of the jar. It is not obvious why there is marked negative geotropism in the laboratory but not in nature. The counter action of the light does not sufficiently explain this fact.

5. SUMMARY

1. *Luffia ferchaultella* is a small wingless Psychid moth that lives on tree trunks, depending for food and a protective case upon lichens growing there. The species, age, position and algal-lichen flora of the tree all affect the moth population.

2. Light intensity influences the distribution of the larvae on the trees.

3. The general distribution of the species in England was mapped, mainly from collected samples. A large number of new locality records was obtained. The moth was not found on hills above 400 ft., nor outside the range of the average July isotherm of 62° F., except in places where there is an average of more than 210 hr. sunshine in July.

4. Evidence is given that the moth is dispersed from tree to tree by wind, that it can go at least several miles, and that mass migrations of larvae from

one part of a tree trunk to another occur, associated with high density of the population.

5. Activity of the larvae was investigated experimentally, and it was found that they were inactive below 40° F. (4° C.), that they were positively phototropic, with a preference for red light, and that they were negatively geotropic in the laboratory (though apparently not in nature). Humidity also effects activity.

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THE COLONIZATION OF A NEW ROCKY SHORE AT PLYMOUTH

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1. Introduction

In the summer of 1935, during the construction of the new Tinside swimming pool at Plymouth, a beach of clean new stone was made round the outside of the pool; and this beach, together with the concrete outer surface of the wall of the swimming pool, gave an excellent opportunity for observation of the process of colonization of a rocky shore on a fairly large scale. Previous workers have studied the colonization of isolated blocks of stone or other substances, but the only record of the colonization of a complete new beach, of which I am aware, is that of Herpin (1935) on the newly made sandy beach at Cherbourg.

The beach at Tinside was kept under observation for two years, and the species present, and their size and abundance, recorded at intervals. For comparison, a study was made of a very similar stony beach nearby, which was sufficiently long-established to have attained a stable condition. A brief account of this older beach is given in the first part of this paper, and the development of the new beach in the second part.

2. The fauna and flora of the long-established beach

This beach lies below the Biological Station, and a few hundred yards only from the swimming pool. (Projected extensions of the bathing beach and terraces threaten to cover it over.) It is composed of stones, mainly limestone, up to 6 in. or a foot in diameter, the larger ones being scarce and chiefly restricted to the higher levels. The beach is walled in on either side by vertical rocks, of which the barnacle fauna has been described in another paper (Moore, 1936). At its upper end the beach enters a cave, and this fact no doubt accounts for the abnormality of the heights of the upper limits of some of the species on the beach, since the reduction in light intensity will reduce the algal growth, and this in turn will affect those animals which rely on the algae for either food or shelter. In any case, the purpose of the present survey was to show what species were abundant in the long-established beach, and not to deal in detail with their zonation.

The method used in the survey was to divide the beach transversely into 2 m. strips, and to note all the species seen in each strip. The mid-level of each strip was then determined with a dumpy level. The results obtained are

summarized in Table 1. As already stated, the beach was atypical at its upper end, so that no great significance must be attached to the upper limits given there. Further, many of the less noticeable species must have been omitted from the list, since, with a few exceptions, most of the identifications were of necessity made in the field. In this connexion I wish to express my indebtedness to all those workers at the Plymouth laboratory who helped with the survey and identifications, and in particular to Mr G. A. Steven, Mr T. G. Tutin, and Mr and Mrs D. P. Wilson. As the work was done at Plymouth, where a standard collection is kept, no special collection was retained.

Table 1. *Fauna and flora of the long-established beach (levels are in metres and refer to ordnance datum)*

Species	Lower limit	Upper limit
ALGAE		
PHAEOPHYCEAE		
Fucus serratus L.	< −3·33	−1·49
F. vesiculosus L.	−2·22	−0·78
Laminaria cloustoni Edm.	< −3·40	−3·40
L. digitata Lamour	< −3·40	−3·40
L. saccharina Lamour	< −3·40	−2·65
Ascophyllum nodosum Le Jol.	−2·75	−1·49
Ectocarpus sp.	Various levels	
RHODOPHYCEAE		
Porphyra umbilicalis Kutz var. *laciniata* J. Ag.	< −3·40	−1·81
Gigartina stellata Batt.	< −3·40	−1·63
Calliblepharis lanceolata Batt.	< −3·40	−3·40
Rhodymenia palmata Grev.	< −3·40	−3·40
Callophyllis laciniata Kutz.	−2·65	−2·65
Laurencia obtusa Lamour	−3·33	−3·33
Ceramium rubrum Ag.	−2·75	−1·63
Lomentaria articulata Lyngb.	−2·65	−2·12
Lithophyllum sp.	−2·22	−2·02
Polysiphonia sp.	−1·63	−1·49
CHLOROPHYCEAE		
Enteromorpha sp.	< −3·40	−0·78
Ulva lactuca L.	< −3·40	−1·07
Lichaena sp.	−2·12	−0·78
PORIFERA		
Grantia compressa (Fabr.)	< 3·40	−2·12
Halichondria panicea (Pallas)	< −3·40	−2·02
Sycon coronatum (Ellis & Sol.)	−2·75	−2·75
COELENTERATA		
Dynamena pumila (L.)	< −3·40	+0·17
Actinia equina L.	< −3·40	+0·17
Tealia felina (L.)	< −3·40	−3·33
Anemonia sulcata (Pennant)	−3·40	−3·40
ANNELIDA		
POLYCHAETA		
Spirorbis borealis Daudin	< −3·40	−1·04
Pomatoceros triqueter (L.)	< −3·40	−1·07
Lanice conchilega (Pallas)	−3·33	−3·33
Nereis cultrifera (Grube)	−3·40	−2·65
N. pelagica L.	< −3·40	−2·75
Lagisca extenuata (Grube)	< −3·40	−2·75
Odontosyllis ctenostoma Clap.	−3·03	−3·03
Eunice harassi Aud. & Edw.	−3·40	−3·40
Audounia tentaculata (Mont.)	−3·40	−2·65
Cirratulus cirratus (O. F. Müller)	−2·65	−1·04

Table 1 (*continued*)

Species	Lower limit	Upper limit
PLATYHELMINTHES		
Fecampia erythrocephala A. Giard	−1·04	−1·00
ECHINODERMATA		
Amphipholis squamata (Della Chiaje)	−3·03	−2·65
CRUSTACEA		
Ligia oceanica (L.)	−2·22	+2·07>
Idotea baltica (Pallas)	−1·81	−1·81
Jaera marina (Fabr.)	−2·75	−1·04
Gammarus marinus Leach	−2·22	−1·04
G. locusta (L.)	−3·40	−2·02
Talitrus saltator (Mont.)	+0·98	+2·07>
Melita palmata (Mont.)	−3·40	−1·07
Apherusa jurinei (H. M.-Edw.)	−2·75	−1·20
Balanus balanoides (L.)	−3·40	−0·78
B. crenatus Brug.	< −3·40	−2·43
B. perforatus Brug.	−3·40	−2·12
Verruca stroemia (O. F. Müller)	−3·40	−2·12
Porcellana platycheles (Penn.)	< −3·40	−3·40
P. longicornis (L.)	< −3·40	−3·40
Eupagurus bernhardus (L.)	−3·40	−3·40
Cancer pagurus L.	−3·40	−2·75
Carcinus maenas (Penn.)	< −3·40	+0·39
INSECTA		
Lipura maritima Guérin	−1·04	−0·15
MOLLUSCA		
Gibbula umbilicalis (da Costa)	−3·40	−2·02
G. cineraria (L.)	< −3·40	−1·81
Littorina littorea (L.)	−3·33	−1·00
L. rudis (Maton)	−2·75	+0·39
L. obtusata (L.)	−2·43	−1·04
L. neritoides (L.)	−1·27	−1·27
Patella vulgata L.	< −3·40	−1·04
Purpura lapillus L.	−3·40	−2·02
Nassarius reticulatus (L.)	< −3·40	−3·40
Trivia monacha (da Costa)	< −3·40	−3·40
Cingula cingillus (Mont.)	−2·12	+0·98
Leucopepla bidentata (Mont.)	−1·49	+0·17
Phytia myosotis (Draparnaud)	+0·39	+2·07
Lamellaria perspicua (L.)	−3·40	−3·33
Goniodoris nodosa (Mont.)	−3·40	−3·40
Heteranomia squamula (L.)	< −3·40	−2·12
Mytilus edulis L.	−3·40	−1·63
Tapes sp. (juv.)	−2·65	−2·65
POLYZOA		
Membranipora sp.	−3·33	−1·20
TUNICATA		
Tridemnum tenerum Verrill	< −3·40	−3·40
Botryllus schlosseri (Pallas)	< −3·40	−2·75
Dendrodoa grossularia (van Beneden)	−2·22	−2·22

As will be seen from the list, the fauna and flora are quite typical of a beach subject to a certain amount of estuarine influence. The sessile species had, in general, not grown to so large a size on the small stones as on the bigger rocks, since the former are liable to be overturned both by people collecting, and by winter storms. However it was clear that there were ample larvae available to colonize any suitable habitat. The occurrence of the two pulmonate molluscs,

Phytia myosotis and *Leucopepla bidentata*, is worthy of note. Both were abundant, together with *Cingula cingillus*, in the upper levels of the shore, but their distribution seemed to vary from time to time, and when the survey was made they were not recorded from levels nearly as high as those at which they had been found on previous occasions.

3. Fauna and flora of the new beach

The stone from which the new beach was made is limestone, and was blasted from the position now occupied by the swimming pool, so that it may be considered as sterile when laid down. The outer face of the pool is concrete, and was completed about the end of May, 1935. The tipping of stone on to the beach was completed by the end of August of the same year. There was a certain amount of shifting of the stones on the beach by wave action, particularly during the first winter; and also, towards the end of the period of observation, by boys looking for crabs. No exact details of level have therefore been attempted, but most of the new beach lies between low water of ordinary neap tides and mid-tide level, while the pool wall rises well above high water.

At first there was no fine material among the stones of the beach, but by August 1937 a definite muddy gravel was beginning to accumulate under the stones, together with its typical fauna of polychaetes, etc. The beach below the Biological Station faces roughly south, while the new one faces east to south-east and is slightly sheltered to the south by a reef; but the difference in wave exposure of the two beaches is probably not great. Detailed notes on the several species are given below, the general progress of colonization being discussed later. The beach was examined on the following dates: 9 and 15 November 1935; 8 February, 23 April, 21 August, and 2 November 1936; 1 March and 23 August 1937.

Fucus serratus.[1] First appeared in March 1937 on the stones on the shore, where plants up to 10 cm. long were found. Unless some of the small unidentified *Fucus* seen on the stones the previous November were this species, they must have grown there since that date. In August 1937 conditions on the stones were similar, *F. serratus* still being scarce, but on the part of the wall kept damp by an outfall from the pool, plants of *F. serratus* up to 30 cm. high were fairly common. These must have grown there since March, because none were seen then.

Fucus vesiculosus. With the exception of a small plant of *Fucus* (sp.?) on the wall of the swimming pool in November 1935, no fucoids of any sort were seen until November 1936. By then a few plants of *F. vesiculosus* up to 25 cm. long were growing on the walls, and a few small plants (sp.?) on some of the rocks. As none were seen on the wall in August 1936, this considerable growth must have taken place within about two and a half months. In March 1937 conditions showed little change, but by August the plants on the wall were more abundant, and some had attained a length of 30 cm.; and some too were fruiting. On the rocks there were still only a few small plants.

[1] Species authorities are only inserted in the text for species not in Table 1.

Fucus spiralis L. var. *platycarpus* Thur. A lot of small plants, 2–5 cm. long, were found on the wall in March 1937. They were not recorded from there the previous November, nor were any seen in August 1937, so they would appear to have been a temporary colonization which did not survive.

Pelvetia canaliculata Dene. et Thur. One or two small plants about 3 cm. high, which were seen on the wall in March 1937, but not either the previous November or the following August.

Himanthalea lorea Lyngb. Some small buttons of this species were found under stones near low water in November 1936, but not recorded subsequently.

Laminaria digitata. A few small plants about 10 cm. long were found on rocks at low water in March 1937. These might possibly have been washed in on stones from deeper water during the winter. They were not noticed the previous November.

Porphyra umbilicalis var. *laciniata.* One of the first colonizers of both wall and rocks. In November 1935 it was present on both, though smaller on the rocks than on the wall. In February 1936 plants up to 10 cm. long were common on the wall, and conditions were very similar in April and August. The plants became very dry during the summer, and are noted as much reduced in numbers in November 1936. In March 1937 they were again abundant and generally distributed on both rocks and wall; but in August they again showed the effect of desiccation on the wall, while remaining abundant and well grown on the rocks, where the lower tidal level, and greater shelter from the sun, resulted in less desiccation. Knight & Parke (1931, p. 77) note that this alga "can withstand considerable exposure but is frequently destroyed in summer when calm sunny weather prevails".

Rhodymenia palmata. Fairly common, and up to a length of 15 cm., on rocks at low water, in August 1937, but not seen there the previous March.

Bangia fuscopurpurea Lyngb. Identified as forming a considerable part of the felt on the wall in November 1935, and, although not specifically identified thereafter, was probably present.

Enteromorpha sp. Probably both *E. compressa* (L.) and *E. intestinalis* (L.) were present. *Enteromorpha* was found on both wall and rocks at the earliest examination in November 1935, and young plants comprised much of the algal felt covering the wall. In February 1936, plants on the wall were recorded up to 30 cm. long, and at all subsequent examinations they were abundant on both rocks and wall, and particularly well grown on the latter in the damp region near the outfall.

Ulva lactuca. Scattered, but common, on both wall and rocks from the first examination in November 1935. Became rather more abundant the following year, and is noted as becoming very dry on the wall in summer.

Grantia compressa. A few small ones seen under rocks in November 1936 but not subsequently.

Halichondria panicea. A single colony, 4 cm. in diameter, was found under a rock in April 1936, and good-sized masses were present in small numbers under rocks in August 1937.

Sycon coronatum. A few small ones found under rocks in November 1936 and some very small ones in August 1937.

Dynamena pumila. First noted as a good growth on rocks in August 1936, but may have been present before this. Remained common thereafter.

Actinia equina. The only sea-anemone found in the area at any time was a small specimen of this species, about 5 mm. in diameter, under a stone in April 1936.

Spirorbis borealis. None was found in November 1935, but by the following February they were abundant and well grown under the rocks, and remained so throughout the observations. In August 1937 there was a heavy settlement of very small individuals, presumably 1937 spat.

Pomatoceros triqueter. In November 1935 these were fairly abundant under the rocks, and ranged in length up to 15 mm. By February 1936 they were more numerous, and ranged up to 20 mm., and by April of that year they were fully grown. Thereafter all sizes were abundant under stones.

Serpula vermicularis L. One or two found, along with *Pomatoceros*, under stones, in August 1937.

Nereis pelagica, *Harmothoe* sp., *Glycera* sp., *Polydora* sp. When a muddy gravel began to accumulate under the stones on the beach, all these worms appeared in numbers in it, or in the muddy water under the stones. They were first recorded in August 1937, and were mostly too young for positive identification. The *Polydora* in particular were particularly abundant.

Membranipora sp. First appeared on the underside of stones in November 1936, and thereafter was very abundant there.

Bowerbankia sp. Some was found under stones in August 1937.

Amphipholis squamata. Appeared very abundantly in the muddy gravel under stones near low water in August 1937, was not seen there previously.

Balanus balanoides. Spat-fall of this species of barnacle usually occurs about April–May, although a few larvae may settle later in the year. The 1935 spat-fall seems to have missed the beach except for a very few individuals which were found under stones in April 1936, at a length of about 7 mm., and one or two seen on the wall in August and November 1936 at 7 and 8 mm. respectively. The 1936 spat seems to have settled later on the rocks and wall than it did on the long-established rocks of the neighbouring reefs where it was abundant in April, although not yet present on rocks or wall. Later a certain number settled on the latter, and in August 1936 and again in March 1937 they are recorded as fairly common on the rocks, and sparsely distributed on the wall, and about 6 mm. long in the latter habitat. By August 1937 this 1936 brood was still present in small numbers on the rocks, and a few survived on the wall also. The 1937 brood had by then settled in considerable quantities, although nowhere sufficiently to produce the overcrowding found on the neighbouring reefs. The general impression gained was one of small density of settlement of larvae and rather poor survival rate on both wall and rocks, but of normal growth rate among those which did survive.

Balanus crenatus. A few, about 8 mm. long, were found under rocks near low water in August 1936, and they were common there in November. These were most probably 1936 spat. In August 1937 well-grown individuals were present there in small numbers.

Balanus perforatus. One, about 5 mm. in diameter, was found under a stone in April 1936. In November a few more were found, apparently falling into two size groups of 5 and 9 mm. means, but it is very doubtful whether this signifies two year groups. In August 1937 small individuals were still present in small numbers under stones.

Chthamalus stellatus (Poli). No 1935 spat settled, but in November 1936 a fair quantity of the 1936 spat was found on the wall, mostly settled in patches cleared by *Patella*. They averaged 2 mm. long, the largest being 4 mm. The following March they are recorded as generally distributed on the wall, but less common than *Balanus balanoides*, and the maximum size found was 5 mm. Conditions were very similar in August 1937, very few of that year's spat having settled, it being rather early in the season for them.

Verruca stroemia. Two specimens were found in November 1935 on a *Gibbula cineraria* under a stone, but this had probably migrated in from another area. Thereafter none was seen until August 1937 when young individuals were found in small numbers under stones at low water. They were probably the spat of that year, since Bassindale (1936) says that this species breeds at Plymouth some time between March–April and September.

Porcellana platycheles. A few small ones were found under stones in April 1936. Throughout

that year they were scarce, but by August 1937 all sizes were present and common under stones near low water.

Porcellana longicornis. A few were found, for the first time, under stones, in August 1937.

Galathea squamifera Leach. One was taken under a stone at low water in August 1937.

Cancer pagurus, Portunus puber (L.). A few small specimens of both these crabs were found under stones from February 1936 onward.

Carcinus maenas. Several were found under stones in November 1935, and by the following April they were quite common, and remained so throughout the observations. With this, and other active species, it is probable that much of the colonization was by well-grown animals, and not only by larvae.

Gibbula umbilicalis. A single specimen was found under a stone in November 1935, but thereafter none was seen until March 1937, when they were fairly common under stones near low water, although considerably less common than *G. cineraria.* The same was true in August.

Gibbula cineraria. This was the commonest Gastropod on the rocky part of the shore. Good-sized individuals were common throughout the period of observation, from November 1935 onward, and their abundance at that early date suggests that they must have migrated in when full grown.

Littorina rudis. Little is known of the growth rate or general biology of this Gastropod. It is viviparous, and presumably its only means of dispersal is by crawling from one place to another, except in so far as the small individuals may be carried about by wave action. In November 1935, a single specimen was seen on the wall, having presumably crawled there from outside. The following February, a few were to be found all over the wall, living in crevices, and mostly having a space of 1–3 cm. cleared from the algal felt round the crevice. In April 1936 they had attained an average height of 6 mm., and few larger than this were ever found on the wall, the largest recorded being 9 mm. From April on they were fairly common all over the wall, but none was taken on the rocks.

Littorina obtusata. One or two were found on weed growing on the rocks, and on the rocks themselves, in November 1936. In August 1937 they were present in small numbers on the rocks, but not in nearly such abundance as on the neighbouring reefs.

Littorina neritoides. These were first found in March 1937, when individuals up to 3·8 mm. high were fairly common in the upper crevices on the wall.

Patella vulgata (including var. *intermedia* and var. *depressa*). According to Lebour (1937) the principal breeding period of this limpet is in the winter, and Orton (1928) records spat of 2–8 mm. in length as being common at Plymouth in June. In November 1935 no spat were seen on the wall, although very small ones may have been present among the algal felt. In February 1936 however, they were present on the wall in considerable numbers, and at a length of 5–15 mm. One or two of the largest of these had probably migrated in from the surrounding reefs, but the rest had almost certainly settled as larvae. By April 1936, the young on the wall, presumably the 1935 brood, averaged 15 mm. long, and a few were as much as 20 mm. In August they ranged from 25 to 30 mm., and in November the largest were 37 mm. long. No young of the 1936 brood were found at that time, but in August 1937, small individuals of 5–15 mm. were common on the wall. The larger ones were then being taken by boys, so the average size could not be determined. In April 1936, a single specimen, 15 mm. long, was taken on a stone, and by August 1937, all sizes were fairly common on the rocks. The high growth rates indicated by these figures confirm Orton's results. His figures of 26–35 mm. long at one year old in 1912, and 11–27 mm. in 1913 at the same age, compared with 6–9 mm. at St Malo (Hatton, 1936), indicate much more favourable growing conditions at Plymouth.

Cingula cingillus. Full grown specimens were very numerous under stones in August 1937, but none was recorded previous to that date.

Heteranomia squamula. None was seen in November 1935, but the following February they were very abundant, at a diameter of about 5 mm., under stones. By August 1936 they had grown to about 10 mm. diameter, which seemed to be their upper limit in this locality. At all times after February 1936 they were abundant under stones.

Mytilus edulis. A few, about 5 mm. long, presumably 1936 spat, were found under stones in August 1936. In November these averaged about 10 mm., and in August 1937 they ranged from 2 to 15 mm., and were fairly common, having probably been added to by a later spat-fall. Orton's figures for Plymouth, in 1919, are 35–40 mm. long at one year old, but only 13–16 mm. at two years on a wave-exposed shore. The rate observed at Tinside lies between these values, but the shells were clean and smooth and not of the rough, stunted type usually associated with a wave-exposed shore.

Botryllus schlosseri. In November 1935, several one-star colonies were found under stones at low water. In February 1936 they were common, and one colony measuring 40 by 40 mm. was found. By August 1936, colonies up to 120 mm. in diameter were common, and thereafter this species was present under most stones near low water.

Botrylloides leachii Savigny. Colonies were found for the first time, and very abundantly, under stones, in August 1937.

4. The general process of colonization

Kitching (1937, p. 484), summarizing previous work on recolonization in the littoral zone, says: "No generalization can be made from the work described above, except that it leads to the impression that recolonization is a somewhat haphazard process, in which the sequence is determined largely by the order of arrival of pelagic larvae and spores. Little evidence has been brought forward to suggest that the establishment of one organism assists either in the establishment or in the elimination of any other." Later, summarizing his own results, this time in a sublittoral habitat, he says (p. 494): "It is concluded that those sessile organisms which finally become established eliminate their predecessors by smothering them or by occupying all the space available for anchorage. The earlier arrivals do not appear to facilitate in any way the establishment of the later ones, except in so far as they form a substratum for them. The slower growing but persistently spreading perennials eventually triumph. It is also concluded that the chief factors which influence the sequence of appearance of mature organisms upon a denuded rock area are (*a*) the time of arrival of spores or larvae of species viable under existing conditions, and (*b*) the growth rate of these species under these conditions." Hatton (1932), on the other hand, has shown that young *Fucus vesiculosus* will not survive unless kept damp either by older plants of the same species or by a felt of *Enteromorpha*.

While it is true that this same sequence of *Enteromorpha* felt followed by Fucoids was observed at Tinside, it was nearly two years after the completion of the wall that Fucoids began to be abundant, while the *Enteromorpha* felt was present almost from the first. And, as Fucoid spores must have been present almost throughout the year, it would appear that some other factor

deterrent to their establishment was operative, though what this was is not apparent. *Enteromorpha*, *Ulva* and *Porphyra*, on the other hand, seem to have found the environment congenial from the first.

Of the attached, suspension-feeding animals, *Spirorbis* and *Pomatoceros*, and the lamellibranch *Heteranomia*, settled in large numbers from the start, and to a lesser extent also, *Botryllus*. The various barnacles, with their more limited breeding seasons, did not appear until the second summer, and then not in nearly such great numbers as on the neighbouring reefs. This is of interest, since several authors speak of the great numbers of barnacle spat settling on test material newly placed in the sea. On the wall they may have found some difficulty in finding space in the thick algal felt, and this is also suggested by the fact that they were thickest in the spaces browsed clear by *Patella*, but this felt was not so thick on the rocks lower on the shore, and it looks as if new limestone rock, which has not been weathered by contact with the sea, does not form a really attractive surface for the attachment of young barnacles. Once settled, their growth appears quite normal for the locality. Finally, sponges, which are quite common on the neighbouring long-established beach, were markedly slow in appearance at Tinside, even after two years, and sea-anemones hardly appeared at all.

Of the deposit- and alga-eating forms, there is in most cases more doubt as to their origin. The *Patella*, which were fairly plentiful at an early date on the wall, must have arrived there as larvae. They seem to have come as soon as there was an algal felt for them to feed on. *Littorina rudis*, which is viviparous, and which also appeared on the wall at an early date, presumably reached the wall as a few adults migrating from another area, and these, breeding rapidly, soon colonized the available space. *Gibbula cineraria* was found fully grown so early, and in such numbers, that there must almost certainly have been a considerable migration of this species from deeper water into the rocky zone near low water. These were probably added to later by larvae settling in the area. It is curious that *G. umbilicalis* should have been so much slower in appearing, and should have remained so much rarer than *G. cineraria*. The young of both species settle in considerable numbers in the sublittoral and lower littoral zones, but the adults of *G. cineraria* usually extend considerably higher on the shore than those of *G. umbilicalis*. It might be expected therefore that the former would show a stronger tendency to migrate up the shore on to the area immediately above low water than would the latter, a similar behaviour having been demonstrated in the several species of *Littorina* occupying different zones on the shore (Gowanloch & Hayes, 1926), and if this were so it would explain the observed facts.

The general impression gained from two years' observation on the colonization of this piece of shore is definitely not one of keen competition for foothold among those species whose larvae are fortunate enough to settle before all the available space is occupied, but rather of a very gradual occupation, with

only some half dozen species capable of finding conditions suitable from the first. To the great majority of those species which were to be expected from comparison with a neighbouring old-established beach, conditions were obviously unsuitable at the commencement of observations, and for many they had not yet become suitable even after a lapse of two years. There is little clue as to what constitutes suitable conditions, but the fact that some species, although sparsely distributed as compared with neighbouring areas, yet showed a normal growth rate, suggests that the difficulty of survival occurs among the newly settled young, and not among the adults.

5. Summary

A newly made stone beach at Plymouth was kept under observation for two years and the progress of colonization noted. A long-established beach close by afforded a standard for comparison. Very few species colonized the beach in any numbers during that time, and it is suggested that the apparently unfavourable conditions affected the newly settled young more strongly than the older individuals.

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THE HABITAT DISTRIBUTION OF BRITISH WOODLAND BIRDS[1]

By DAVID LACK and L. S. V. VENABLES

(*With Plates* 1–3)

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1. Introduction

A paper by Elton (**2**), organized as a result of a broadcast talk in 1933, was the first attempt to classify the habitat distributions of British woodland birds, and he there suggested that a more detailed investigation would be profitable. The band of observers now organized under the British Trust for Ornithology

[1] Publication of the British Trust for Ornithology.

provided a suitable machinery for a more extensive survey applying to all British woodland birds in all the main types of wood in the main geographical regions of Britain. In the present state of knowledge, such a general survey, though necessarily less detailed, was felt to be more valuable than concentrated study on a few species or woodland types. The object of the enquiry was an analysis of habitat distributions, to investigate which factors provided by woods were important in habitat limitations, and to compare the differences in species composition of the different woodland types, as in the admirable study by Palmgren (**9**) for Finland. It should be stressed that the total individual bird populations of woods, with related problems, were not an object of the present enquiry; these are being studied by W. B. Alexander and the Oxford Bird Census. Nor were the geographical distributions of British woodland birds investigated, except where these have some bearing on habitat; this knowledge is summarized in the new *Handbook of British Birds*.

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A summary of each count is given in the Appendix. On account of considerations of space, it was not possible to give full details of each individual count, but the more detailed surveys, such as Mr H. A. Course's weekly walk for a period of over a year through a beech wood, have been deposited with the British Trust for Ornithology for the benefit of future workers.

The writers also wish to thank the members of the scientific advisory committee of the British Trust for Ornithology for supplying further information, not elicited by the counts, on the habitat distribution of rarer species, and also for valuable criticisms during the progress of the work.

3. List of all species mentioned in the text

List of birds mentioned in the text or included in the tables, with the scientific names given in Witherby's Practical Handbook of British Birds (1924), vol. 2, pp. 903–36

Hooded crow (*Corvus cornix*)
Carrion crow (*Corvus corone*)
Rook (*Corvus frugilegus*)
Jackdaw (*Coloeus monedula*)
Magpie (*Pica pica*)
Jay (*Garrulus glandarius*)
Starling (*Sturnus vulgaris*)
Hawfinch (*Coccothraustes coccothraustes*)
Greenfinch (*Chloris chloris*)
Goldfinch (*Carduelis carduelis*)
Siskin (*Carduelis spinus*)
Lesser redpoll (*Carduelis linaria cabaret*)
Linnet (*Carduelis cannabina*)
Bullfinch (*Pyrrhula pyrrhula*)
Crossbill (*Loxia curvirostra*)
Chaffinch (*Fringilla coelebs*)
Brambling (*Fringilla montifringilla*)
House sparrow (*Passer domesticus*)
Tree sparrow (*Passer montanus*)
Yellow bunting (*Emberiza citrinella*)
Cirl bunting (*Emberiza cirlus*)
Woodlark (*Lullula arborea*)
Tree pipit (*Anthus trivialis*)
Meadow pipit (*Anthus pratensis*)
Grey wagtail (*Motacilla cinerea*)
Tree creeper (*Certhia familiaris*)
Nuthatch (*Sitta europoea*)
Great tit (*Parus major*)
Blue tit (*Parus coeruleus*)
Coal tit (*Parus ater*)
Crested tit (*Parus cristatus*)
Marsh tit (*Parus palustris*)
Willow tit (*Parus atricapillus*)
Long-tailed tit (*Aegithalos caudatus*)
Goldcrest (*Regulus regulus*)
Spotted flycatcher (*Muscicapa striata*)
Pied flycatcher (*Muscicapa hypoleuca*)
Chiffchaff (*Phylloscopus collybita*)
Willow warbler (*Phylloscopus trochilus*)
Wood warbler (*Phylloscopus sibilatrix*)
Garden warbler (*Sylvia borin*)
Blackcap (*Sylvia atricapilla*)
Whitethroat (*Sylvia communis*)
Lesser whitethroat (*Sylvia curruca*)
Fieldfare (*Turdus pilaris*)
Mistle thrush (*Turdus viscivorus*)
Song thrush (*Turdus philomelus*)
Redwing (*Turdus musicus*)
Ring ouzel (*Turdus torquatus*)
Blackbird (*Turdus merula*)
Redstart (*Phoenicurus phoenicurus*)
Nightingale (*Luscinia megarhyncha*)
Robin (*Erithacus rubecula*)
Dunnock or hedge sparrow (*Prunella modularis*)
Wren (*Troglodytes troglodytes*)
Nightjar (*Caprimulgus europoeus*)
Green woodpecker (*Picus viridis*)
Great spotted woodpecker (*Dryobates major*)
Lesser spotted woodpecker (*Dryobates minor*)
Wryneck (*Jynx torquilla*)
Cuckoo (*Cuculus canorus*)
Little owl (*Athene noctua*)
Long-eared owl (*Asio otus*)
Tawny owl (*Strix aluco*)
Barn owl (*Tyto alba*)
Hobby (*Falco subbuteo*)
Kestrel (*Falco tinnunculus*)
Buzzard (*Buteo buteo*)
Sparrow hawk (*Accipiter nisus*)
Heron (*Ardea cinerea*)
Ring dove or wood pigeon (*Columba palumbus*)
Stock dove (*Columba oenas*)
Turtle dove (*Streptopelia turtur*)
Woodcock (*Scolopax rusticola*)
Moorhen (*Gallinula chloropus*)
Capercaillie (*Tetrao urogallus*)
Blackcock (*Lyrurus tetrix*)
Pheasant (*Phasianus colchicus*)

4. Definition of a woodland bird

In this enquiry, observers were asked to record every bird which they saw in the woods that they investigated, and nearly all these species are recorded in the tabulated counts in the Appendix. However, to save space the sporadic records of species, such as the meadow pipit, which are typical of open ground without trees, and whose occurrence in woods is accidental and without significance, were omitted from these counts.

A further group of species was included in the Appendix, but are omitted from all detailed analysis in the present paper since, though they typically frequent trees or scrub, they are not typical of woods, and, when they occur

there, are almost exclusively on the wood edge. They are typical of open country with scattered trees or scrub, and are hardly to be considered woodland birds.

Table 1. *Species of the wood edge omitted from further consideration*

Magpie*	Woodlark
Greenfinch	Lesser whitethroat
Goldfinch	Wryneck
Tree sparrow	Cuckoo*
Yellow bunting	Turtle dove*
Cirl bunting	

* Magpie, cuckoo and turtle dove are fairly common in woods, but, like the rest, are *primarily* birds of more open country.

It should be emphasized that only a very arbitrary line can be drawn between those species which were omitted and those included. A "woodland bird" cannot be strictly defined, and other workers might make a different division. The birds of open country with scattered trees given in Table 1 grade insensibly into those frequenting parkland, with well-spaced trees at regular intervals, and so to those of very open woods. Again, certain "woodland" species, such as the tree pipit and various birds of prey, require only a single tall tree (either as a song post or for nesting), and so should not perhaps be included as woodland birds. But such of these birds as also occur regularly when there is more than one tree have been included as woodland birds in this paper. Again, a number of species obtain only some of their requirements, or a single one, in the wood, and other requirements, e.g. food, exclusively outside the wood. The occurrence of various species in woods is correlated with very different factors, and some of these species commonly, others only rarely, find all these requirements satisfied in situations outside woods. Even so typical a woodland species as the blackbird breeds in treeless areas in Shetland (Venables) and on Ailsa Craig (J. Fisher), feeding on grass moor, nesting in sheltered cracks or ledges in stone walls and rock-sides, and singing from the tops of stone walls and crags; all its requirements are satisfied without a single tree. Another difficulty is presented by such species as willow warbler and wren, which are really scrubland species; but since most scrubland in Britain to-day is found in woods, these are two of the commonest birds in woods; but they do not require any trees in their habitat, though they may use them when present. Hence it is difficult to say whether they should be considered as woodland birds.

It is clear that the term "woodland bird" is an artificial one. Different species of birds have different requirements, and these are satisfied to a greater or less degree by the habitat we term a wood. Probably, in earlier times, the birds of the natural forest land would have been much more sharply divided from those of other natural habitats, though there would still have been some overlap. But in Britain to-day there is almost no surviving natural forest

land, and the birds of the planted woodlands are not at all clearly demarcated from those of other man-made habitats such as orchards, gardens, parks, and hedgerows with tall trees.

5. THE REQUIREMENTS OF WOODLAND BIRDS

The requirements of the different woodland species are set out in Table 3. It saves space to tabulate separately those species which feed almost exclusively outside woods but which use trees (sometimes but by no means always in woods) for nesting sites. The requirement of these species is not a wood but one or more tall trees.

Table 2. *Species nesting in trees and feeding outside woods*

Rook	Hobby
Little owl	Heron
Kestrel	

N.B. Quite a number of other British birds occasionally nest in trees; only the most regular species have been included in Table 2.

Of the species in Table 2, the kestrel also breeds regularly on cliffs and the little owl in many types of holes outside woods, e.g. rabbit burrows. Rook and heron, being social, usually nest in a group of trees, both in woods and in isolated clumps. The hobby, which nests much more frequently in conifers than in broad-leaved trees, is essentially a bird of open country with trees, but does sometimes nest in woods. Hence some of these species might not be considered "woodland birds". Once again there is only an arbitrary line between these and such species as carrion and hooded crows, jackdaw, starling, stock and ring doves; all the latter have been included in Table 3, for though all of them except the ring dove breed commonly away from trees in some areas, when they do occur in woods they obtain much of their food there.

In Table 3 the requirements and niches of the different species have been classified so far as at present known, as these are essential for the appreciation of the later sections. The most fundamental divisions of the wood are the leaf canopy, the timber (by which is meant the trunk and main branches), the secondary growth, the ground, and the air between the canopy and the ground. *In Table 3 only those niches frequented most characteristically by each species have been tabulated.* If occasional or exceptional records were included, many more crosses would have to be added in each column, and this would destroy the typical picture which Table 3 is intended to present.

For a fuller ecological picture, both the food and the winter roosting places should have been added. Neither of these was made an object of the present enquiry. Much information on the food of British birds is available in the works of Collinge (**1**), Jourdain (**3**) and others. In many species too little is known about roosting for any generalizations to be made. The table shows the great diversity in the requirements of the various woodland species.

Table 3. *Typical niches of woodland birds*

Species	Breeding season: Nests: Canopy	Nests: Holes	Nests: Secondary	Nests: Ground	Sings*: Air	Sings*: Canopy	Sings*: Timber	Sings*: Secondary	Sings*: Ground	Feeds: Air	Feeds: Canopy	Feeds: Timber	Feeds: Secondary	Feeds: Ground	Winter: Feeds: Canopy	Winter: Feeds: Timber	Winter: Feeds: Secondary	Winter: Feeds: Ground	Remarks
Carrion crow	×	.	.	.	×	×	.	.	.	.	×	.	.	×	.	.	.	×	—
Hooded crow	×	.	.	.	×	×	.	.	.	.	×	.	.	×	–	–	–	–	Not in woods in winter. Commonly breeds in rocks
Jackdaw	.	×	.	.	.	.	.	.	.	.	×	.	.	×	.	.	.	.	Occasional canopy nester. Also commonly breeds outside woods
Jay	×	.	×	.	.	.	.	.	.	.	×	.	×	.	×	.	×	×	Mainly in broad-leaved woods
Starling	.	×	.	.	.	×	.	.	.	×	×	.	.	×	.	.	.	×	Common outside woods
Siskin	×	.	.	.	×	×	.	.	.	.	×	.	.	.	×	.	.	×	Summer in coniferous, winter in birch-alder
Chaffinch	×	.	×	.	.	×	.	×	.	.	×	.	×	×	.	.	.	×	All types of wood
Brambling	–	–	–	–	–	–	–	–	–	–	–	–	–	–	.	.	.	×	Predominantly in beech in winter. In Scandinavia nests in pine and birch
Lesser redpoll	×	.	.	.	×	×	.	.	.	.	×	.	.	.	×	.	.	×	Predominantly in birch-alder
Hawfinch	×	.	.	.	.	×	.	×	.	.	×	.	×	×	×	.	×	×	—
Bullfinch	.	.	×	.	.	.	.	×	.	.	×	.	×	.	×	.	×	.	Scrub species
Crossbill	×	.	.	.	.	×	.	.	.	.	×	.	.	.	×	.	.	.	Wood edge for nesting. Conifer only. Near water
Tree pipit	.	.	.	×	×	×	.	.	.	.	.	.	.	×	–	–	–	–	Open woods
Tree creeper	.	×	.	.	.	.	×	.	.	.	.	×	.	.	.	×	.	.	Frequents small branches also. Nests in cracks in bark
Nuthatch	.	×	.	.	.	×	×	.	.	.	?	×	.	.	×	×	.	.	Predominantly in broad-leaved woods
Goldcrest	×	.	.	.	.	×	.	.	.	.	×	.	.	.	×	.	×	.	Predominantly in coniferous woods
Great tit	.	×	.	.	.	×	.	×	.	.	×	×	×	.	×	×	×	×	More numerous in broad-leaved woods
Coal tit	.	×	.	.	.	×	.	.	.	.	×	×	?	.	×	×	×	×	More numerous in conifer woods
Marsh tit	.	×	.	.	.	×	.	×	.	.	×	×	×	.	×	×	×	×	Predominantly in broad-leaved woods
Willow tit	.	×	.	.	.	×	.	×	.	.	×	×	×	.	×	×	×	×	Near marsh or water. Broad-leaved woods
Blue tit	.	×	.	.	.	×	.	×	.	.	×	×	×	.	×	×	×	×	More numerous in broad-leaved woods
Crested tit	.	×	.	.	.	×	.	.	.	.	×	.	.	.	×	×	×	×	Predominantly in coniferous woods
Long-tailed tit	.	.	×	.	.	×	.	×	.	.	×	.	×	.	×	.	×	.	Scrub species

Whitethroat	.	.	×	.	×	.	.	×	.	.	.	.	.	×		–	–	Scrub species
Garden warbler	.	.	×	.	.	×	.	×	.	.		.	.	×			–	Predominantly in broad-leaved woods
Blackcap	.	.	×	.	.	×	.	×	.	.	×	.		×	–			Predominantly in broad-leaved woods
Willow warbler	.	.	.	×	.	×	.	.	.	.	×	.	.	×				Scrub species
Wood warbler	.	.	.	×	.	×	.	.	.	.	.	.	.	×				Predominantly in broad-leaved woods with sparse or absent secondary growth
Chiffchaff	.	.	.	.	.	.	.	.	.	.	.	.	.	.				Mainly in broad-leaved woods
Mistle thrush	.	.	.	.	.	×	.	.	.	.	.	.	.	×	.	.	.	Nests in strong fork, often low down
Song thrush	.	.	×	.	.	×	.	.	.	.	.	.	.	.	×	.	.	×
Blackbird	.	.	.	.	.	×	.	.	.	.	.	.	.	×	×	.	.	×
Redstart	.	×	.	.	.	.	.	.	.	×	.	.	.	.				Open woods for "pouncing"
Robin	.	×	.	×	.	×	.	×	.	.	.	.	.	×	.	.	.	.
Nightingale	.	.	×	×	.	.	.	×	.	.	.	.	.	.	–	–		Predominantly in broad-leaved woods
Dunnock or hedge sparrow	.	.	×	.	.	.	.	×	.	.	.	.	.	.	.	.	.	Scrub species
Wren	.	×	×	×	.	.	.	×	.	.	.	.	.	×	.	.	.	Scrub species. Nests in any hole or crack. Also away from woods and scrub
Spotted flycatcher	.	×	.	.	.	×	.	×	.	.	.	.	.	.	–	–	–	–	Open woods for "pouncing". Nests in ledges or cracks
Great spotted woodpecker	.	×	.	.	.	.	×	.	.	.	.	×	.	.	.	.	.	All types of wood
Lesser spotted woodpecker	.	×	.	.	.	.	×	.	.	.	.	×	.	.	.	×	.	Predominantly in open broad-leaved woods
Green woodpecker	.	×	.	.	.	.	×	.	.	.	.	×	.	×	.	×	.	More numerous in broad-leaved woods
Nightjar	.	.	.	×	.	×	.	×	.	×	.	.	.	.	–	.	–	Open woods for "snapping". Bare earth for nest
Long-eared owl	×	.	.	.	.	×	.	.	.	×	.	.	.	.	.	.	.	Feeds on the wing
Tawny owl	.	×	.	.	.	×	.	.	.	×	.	.	.	.	.	.	.	Feeds on the wing
Sparrow hawk	×	.	.	.	×	.	.	.	.	×	.	.	.	.	.	.	.	Feeds on the wing
Woodcock	.	.	.	×	×	.	.	.	.	.	.	.	.	×	.	.	.	Nests near swamp or stream
Stock dove	.	×	.	.	.	×	.	.	.	.	.	.	.	×	.	.	.	Sometimes nests in rabbit holes outside woods, or in cliffs
Ring dove	×	.	×	.	.	×	.	.	.	.	×	.	.	×	×	.	.	All types of wood
Pheasant	.	.	.	×	.	.	.	.	×	.	.	.	.	×	.	.	.	Uses the trees for roosting
Capercaillie	.	.	.	×	.	×	.	.	.	.	×	.	.	×	×	.	.	Predominantly in coniferous woods
Blackcock	.	.	.	×	.	.	.	.	×	.	×	.	.	×	×	.	.	Open woods. Predominantly in pine and birch

* Or other breeding call.

6. Methods of survey

For describing and discussing woodland distributions, it was desirable to obtain a *comparative index* of the abundance of each species in the different wood types. Although total populations were not an object of the enquiry, the ideal method for obtaining such a comparative index was to have complete censuses taken of a large number of woods of each different type. But such complete censuses would have required an enormous quantity of extremely arduous work, and so few sample woods could have been taken that no generalizations on habitat distribution could have been safely made; nor did any of the various shorter methods for obtaining quantitative results, summarized by Lack (**5**), seem practicable under the circumstances of the present enquiry.

Another method was to ask observers to send in simply a list of all the species found in each wood, with no reference to frequency. On the assumption that the commoner a bird is the more woods it is likely to be recorded from, a comparative frequency index can be obtained from the percentage of woods in which each species occurs. This gives an index of some value, but it was obviously preferable if observers could give some indication of relative abundance. Terms such as common and rare are worse than useless, since they have different meanings for different observers and different species. Therefore each observer was asked to record the actual numbers of each species that he observed during a slow walk through the wood. Where possible, one or more counts were taken later, and in such cases the figure for each species in the Appendix is the largest number of individuals of each species seen on any one walk.

The figures obtained on one sample walk are obviously only a very rough indication of the numerical abundance of the different species. A second count taken soon after the first along the same route often shows considerable differences from the first. Hence the figures must not be used too precisely. Nevertheless, they do present an advance on the bare species list. With these considerations in mind, a comparative index of abundance for each species was obtained as follows. Where only one individual of a species was seen in the walk or walks through a wood it was scored as 1, between two and nine individuals were scored as 2, and over nine were scored as 3. The score of each species in all the woods of the same type was added, and, to make the figures for the different woods comparable, this score was then divided by the number of woods involved. To make a suitable index, the highest number obtained by this method, namely, 2·6 for the chaffinch in Highland pine, was taken as 100, and the other index numbers were calculated in proportion, which means multiplying them by 37·5. The results are given to the nearest ten. Table 4 gives the results.

The method of calculating the index from the figures in the Appendix will be clearer from an example. In the breeding season counts of the 45 oak and

mixed broad-leaved woods, the great tit was recorded singly 6 times (score 6), between 2 and 9 individuals were recorded 21 times (score 42), and over 9 individuals were recorded once (score 3). The total score is therefore $6+42+3=51$. This number is divided by the number of woods, namely, 45, and multiplied by 37·5 to make a suitable index, which gives a figure of 40 when expressed to the nearest 10. In the breeding season counts for pine woods, the index for the great tit works out at 10. From this it may reasonably be inferred that the great tit is roughly four times as abundant in oak woods as pine woods in the breeding season. A similar calculation for the coal tit gives an index of 20 for oak woods and 60 for pine woods, in the breeding season; hence this species shows a frequency as regards oak and pine woods which is almost the reverse of that of the great tit.

The reason for assessing the number of individuals recorded on each count in three arbitrary divisions, scoring respectively 1, 2 and 3, was as follows. Even in the breeding season, woodland birds wander to some extent, hence, if only one individual was seen, it might well be sporadic, and such a record clearly has less value than if two or more individuals were seen, which suggests regularity. The counts were obviously not sufficiently accurate to be treated as they stood, hence all figures between 2 and 9 were grouped together, and were scored as 2. On the other hand, if 10 or more individuals were seen, that species was clearly abundant, and so was scored as 3.

Since a large number of woods of each type was counted, it is claimed that the comparative index of abundance obtained as described does present a fairly accurate picture of British woodland bird distributions, and this picture corresponds with the impressions of the present writers without the subjective errors to which the latter, by themselves, would be liable. To avoid confusion, it should be reiterated that the figures in the Appendix are not complete censuses, and that no greater accuracy is claimed for them than what is needed for obtaining the comparative index as described; while only major differences in comparative index are considered in the subsequent discussion. No method is available for testing the reliability of the index except by taking complete censuses of all the woods concerned. For a closer analysis of habitat distributions, a single group of species might be selected, for which complete censuses might well be practicable, but, as already stated, the object of the present enquiry was a general survey.

When the figures are treated to get only the most obvious differences, as described, one error remains, namely, that certain species, notably the tree-creeper, are less conspicuous than others, and so are relatively too few in the counts. For this reason the counts are used primarily for comparing the distributions of the same species in different habitats, not of different species in the same habitat.

Observers were asked to investigate woods of as pure types as possible (but a few counts from mixed woods were included in the Appendix), and detailed

descriptions of the actual woods counted by each observer have been deposited at Oxford with the British Trust for Ornithology, where those interested can consult them. To save space, only more generalized descriptions are given here.

Counts were taken in both the breeding and the non-breeding season, the former between mid-April and June (at least two counts where possible), the latter for convenience restricted to between November and February. Altogether 152 woods were counted in summer and 120 in winter, of which the two writers themselves counted 50 in summer and 61 in winter. This paper is based not only on these counts, but also on the writers' observations in many other woods, while questions on which further information was required were circulated among a group of experienced field observers.

Discussion of Table 4

Ideally the indices should have been tabulated in a number of separate tables, one in each relevant section of the following discussion, but, on account of space considerations, they have all been placed in one table, in a number of separate sections. Therefore in reading the following discussion, Table 4 should be constantly referred to, as actual figures are not quoted again in the text. While most of the discussion is based on Table 4 (also supported by the general field impressions of the writers), the influence of certain factors, also the distribution of certain uncommon species, cannot be worked out from indices based on the observers' counts. The evidence in these cases is based on the field observations of the present writers together with those of the members of the scientific advisory committee of the British Trust for Ornithology; such cases are clearly specified in the text.

The whole of the first part of the discussion refers exclusively to the breeding season, winter distributions being considered separately at the end.

As shown in Table 4, a few species, notably chaffinch and ring dove, and to a lesser extent tree creeper, mistle thrush, robin and great spotted woodpecker, occur almost equally in all types of woods during the breeding season. But there are quite marked differences in the bird species of the different kinds of woods. Some of these differences seem correlated directly with the species of tree composing the wood, but several other factors are extremely important, and these will be considered first.

7. Some habitat factors

(*a*) *Birds of open as opposed to closed woods*

Certain species of woodland birds occur predominantly in woods where the trees are widely spaced, and when they do occur in woods with a closed canopy are found predominantly on the edges and near rides. It is, naturally, impossible

Table 4. *Comparative index of frequency of woodland birds in different wood types**

	Breeding season											Winter			
	Oak and five mixed broad-leaved	Beech	Birch	Pine and one pine with larch	Larch	Pine + secondary	Pine − secondary	Oak and beech + secondary	Oak and beech − secondary	Pine forest (Highlands)	Pine plantations	Oak and two mixed broad-leaved	Beech	Birch	Pine and one pine with larch
Number of woods ...	45	24	22	33	11	16	17	56	13	9	24	39	18	17	33
Carrion crow	10	×	5	10	10	10	10	10	—	10	10	10	—	—	—
Hooded crow	—	—	—	5	—	—	10	—	—	20	—	—	—	—	—
Jackdaw	10	30	10	—	—	—	—	10	20	—	—	10	5	—	—
Jay	30	20	5	10	20	10	×	30	×	—	10	40	20	10	20
Starling	40	60	10	5	—	5	10	40	50	—	10	10	10	—	×
Siskin	—	—	—	10	—	10	×	—	—	30	—	—	—	10	—
Chaffinch	70	60	70	90	90	80	90	60	70	100	80	30	90	20	10
Brambling	—	—	—	—	—	—	—	—	—	—	—	—	60	—	×
Redpoll	—	×	10	×	—	×	—	—	—	—	×	10	—	50	×
Bullfinch	20	10	5	×	×	×	—	20	—	—	×	20	10	40	5
Crossbill	—	—	—	10	—	10	20	—	—	20	10	—	—	—	20
Tree pipit	×	5	10	10	—	10	20	×	10	40	×	—	—	—	—
Tree creeper	10	20	10	10	30	10	10	10	×	20	10	20	20	5	30
Nuthatch	10	10	×	—	—	—	—	10	5	—	—	20	20	×	—
Goldcrest	5	(5)†	×	50	40	60	40	5	—	50	50	30	—	20	80
Great tit	40	30	20	10	30	20	10	40	20	—	20	50	60	40	10
Coal tit	20	20	30	60	60	70	60	30	×	80	60	40	40	30	80
Marsh + willow tits‡	20	20	20	—	10	—	—	20	10	—	—	50	30	×	10
Blue tit	50	30	40	10	50	10	5	50	10	—	10	70	80	70	30
Crested tit	—	—	—	10	—	10	10	—	—	50	—	—	—	—	10
Long-tailed tit	20	5	10	5	×	5	5	20	—	—	5	50	20	30	10
Whitethroat	30	5	10	5	—	10	—	30	—	—	10	—	—	—	—
Garden warbler	20	10	10	5	×	10	—	20	—	—	5	—	—	—	—
Blackcap	20	10	5	5	×	10	—	20	×	—	10	—	—	—	—
Willow warbler	70	20	80	30	50	50	20	60	—	30	30	—	—	—	—
Wood warbler	10	30	10	×	—	—	×	10	50	—	×	—	—	—	—
Chiffchaff	30	30	10	×	30	5	—	40	—	—	5	—	—	—	—
Mistle thrush	30	20	10	20	×	20	20	30	10	10	30	10	10	—	5
Song thrush	50	40	30	10	30	20	10	50	20	10	10	30	20	10	5
Blackbird	70	70	50	30	50	40	20	70	50	×	40	70	60	20	20
Redstart	×	10	5	20	—	10	20	5	—	50	5	—	—	—	—
Robin	60	50	60	30	50	60	20	60	40	40	30	60	30	30	10
Nightingale	10	5	×	×	—	×	—	10	—	—	×	—	—	—	—
Dunnock or hedge sparrow	20	10	10	10	10	30	—	20	—	×	20	30	10	20	10
Wren	60	30	30	30	30	40	10	50	20	10	30	40	20	20	30
Spotted flycatcher	5	10	5	×	—	5	—	10	10	×	5	—	—	—	—
Great spotted woodpecker	10	10	5	5	×	10	×	10	×	—	10	10	×	5	5
Lesser spotted woodpecker	5	5	×	—	—	—	—	5	×	—	—	5	—	—	—
Green woodpecker	10	20	10	5	10	10	—	20	10	—	5	10	10	10	10
Woodcock	5	—	10	×	—	5	—	×	5	×	×	10	—	10	—
Stock dove	5	10	5	10	—	10	10	10	×	—	20	×	—	—	—
Ring dove	40	60	40	40	70	50	40	50	50	×	60	50	80	20	20
Pheasant	30	10	10	20	20	30	10	30	×	10	20	30	10	5	10
Capercaillie	×	—	—	10	—	20	5	—	5	30	5	—	—	×	10
Black grouse	—	—	10	10	—	×	20	—	—	30	—	—	—	×	5

* The method of obtaining the index is described on pp. 46–7. × indicates a score of 1 whatever the calculated index. A single occurrence is liable to be sporadic. 5 indicates an index of between 3 and 7 when there was more than one occurrence. 10 indicates an index of between 7 and 14. All other indices are calculated to the nearest 10.

† Four goldcrests recorded from beech woods in June had probably moved in after breeding, so this should probably be blank. [N.B. Those in oak woods were breeding.]

‡ Marsh and willow tits were not distinguished by many observers, so were scored together.

to draw any clear line between these species and those given in Table 1, which were so much birds of the wood edge as to be omitted from further consideration. But all the birds characteristic of open woods given in the following list occur regularly right into the interior of woods, provided there is an open canopy:[1]

Crossbill
Tree pipit
Wood warbler
Redstart
Spotted flycatcher
Pied flycatcher
Lesser spotted woodpecker
Nightjar
Blackcock

The tree pipit was the only one of these species invariably recorded from a wood with an open as opposed to a closed canopy. Like the woodlark, it has an aerial song flight from a high perch, and Lack (**4**) and Venables (**15**) show that a high song post is the only factor for which these species require trees. Redstart, spotted and pied flycatchers, and nightjar, when not in woods with an open canopy, require much open space between canopy and secondary growth; in this they catch their insect food on the wing. The nightjar is regular in woods, but also on heathland; the presence of a wood seems immaterial to it, though it uses tall trees for singing and roosting when these are available. The wood warbler should not perhaps have been included in this group. It needs "space", but is characteristic not of woods with an open canopy, but of woods with a closed high canopy with almost no secondary or undergrowth; when it does occur in woods with secondary growth there is nearly always much space between canopy and secondary growth. In this it agrees with the redstart and the flycatchers, but its distribution is correlated not with feeding but with its habit of an aerial song flight from one bough to the next. The black grouse seeks the cover of trees when disturbed, and at times feeds in them, but it also feeds regularly in open country, and normally displays on flat open ground devoid of trees. Crossbill and lesser spotted woodpecker are typical of open woods, but this does not seem correlated with any special habits or adaptations.

(*b*) *Birds dependent on secondary growth*

The term "secondary growth" cannot be precisely defined, since it grades into tall ground vegetation on the one hand and low trees on the other. The term is used here for the bushes, scrub and young trees found as a layer below the canopy trees in many woods, and from 3 to 12 ft. may be taken as its usual height.

In one section of Table 4, indices are calculated separately for birds in

[1] This list is based on the writers' experience. It was impossible to separate out the open from the closed woods from the observers' lists, as so many woods included both open and closed parts, so that index figures could not be compiled. In the observers' counts (Appendix) it may be noted that among pine woods, A 28, 29, 30, 31, 48 and 49 had open canopy throughout, and that all Scottish and North of England birch woods have a predominantly open canopy.

woods with secondary growth and in woods without secondary growth, for both coniferous and broad-leaved woods. It should be noted that almost no wood is completely devoid of secondary growth, hence a few birds typical of secondary growth were recorded in woods classified as without secondary, and some of the woods with secondary growth had some areas without any. Hence the differences dependent on secondary growth are really more marked than this table indicates. (Woods containing young trees and trees with low branches were, of course, included as woods with secondary; hence no birch woods were included as without secondary.)

Table 4 shows clearly that the following species occur typically in woods with good secondary growth and not where this is absent.

Jay	Chiffchaff
Bullfinch	Nightingale
Long-tailed tit	Dunnock or hedge sparrow
Whitethroat	Wren
Garden warbler	Pheasant
Blackcap	Capercaillie
Willow warbler	

The height of secondary growth required differs for the different species (based on field observations). Wren, pheasant and capercaillie require tall ground vegetation rather than secondary growth. Most of the others require secondary growth at least about 4 ft. high, the nightingale and garden warbler at least about 8 ft. and the jay typically higher than these. At this stage other species, such as robin and song thrush, might have been included. The series grades into species frequenting lower trees, so that no definite line can be drawn. (For the stage at which different species colonize trees of different heights see the studies of young plantations by Schiermann (**12**), and Lack (**4**).)

Of the thirteen species in the above list, nine are typical of scrub or secondary growth (of the heights already given) outside woods, and so are not dependent on woods as such. Of these nine species five, namely, bullfinch, whitethroat, nightingale, dunnock and wren, *tend* to keep mainly in the secondary growth for all their activities in the breeding season even when they are nesting in woods. Of the other four species, the long-tailed tit feeds in the trees, the pheasant roosts there and garden and willow warblers sing (and to some extent feed) there, when they breed in woods, but for none of these are canopy trees essential. But blackcap and chiffchaff, unlike their relatives the garden warbler and willow warbler respectively, do not occur in scrub outside woods unless there are also a few tall trees. For these two species one (and, at least for the blackcap apparently, only one) essential requirement is supplied by woods, namely, the tall song posts afforded by canopy trees. Although both blackcap and chiffchaff at times sing lower down in their territories, each territory investigated had some taller song posts, hence these species are found typically only in woods; whereas the minimum height of song post required by garden and willow warblers is satisfied by secondary growth. Blackcap and

chiffchaff utilize secondary growth for nesting, also for cover and feeding; the chiffchaff also feeds a great deal in the canopy. The remaining two species, jay and capercaillie, are arboreal in many of their habits, and do not occur in secondary growth outside woods.

The species discussed above are almost confined to woods with good secondary growth. Table 4 shows that although some other species are commoner in such woods, they also occur, though less frequently, in woods without secondary growth. This is true of the hole-nesting tits which are also commoner in open woods without secondary growth (including parks) than in closed woods. Song thrush and robin are also commoner in, but by no means confined to, woods with good secondary growth, the former nesting in it, the latter using it for feeding and cover. The robin, like the wren, also occurs in woods devoid of secondary growth when there are rocks or stone walls, which they use for nesting and also feeding. The wren even occurs in many rocky areas devoid of both trees and bushes.

Table 4 also shows three species to be much commoner in woods devoid of secondary growth than in woods where it is present, namely, tree pipit, wood warbler and redstart. The tree pipit, except for its tall song post, is essentially a ground bird, like the meadow pipit. Wood warbler and redstart have already been discussed; they do occur in woods with secondary growth, but require much open space, hence are commoner in woods where secondary growth is scarce. Not enough figures were available for the nightjar, but it also is typical of woods without secondary growth. In addition to requiring much space for feeding, it also nests on bare ground.

(*c*) *Hole-nesting birds*

The following species nest in holes and are therefore scarce in or absent from younger plantations and are particularly common where there are old trees:

Jackdaw	Crested tit
Starling	Redstart
Tree creeper (cracks)	Spotted flycatcher (ledges)
Nuthatch	Pied flycatcher
Great tit	Great spotted woodpecker
Coal tit	Lesser spotted woodpecker
Marsh tit	Green woodpecker
Willow tit	Tawny owl
Blue tit	Stock dove

(Also tree sparrow and wryneck in Table 1, and little owl in Table 2.)

Of the above species, jackdaw, starling and stock dove, and, to a lesser extent, the tawny owl, regularly nest outside woods in other kinds of holes. The others are more truly woodland birds; but many of them will nest in artificial holes in woodwork (especially in nesting boxes or holes in buildings), and nuthatch, coal, marsh and blue tits nest occasionally in holes in stonework. The

coal tit also nests not infrequently in holes in banks or even in the flat ground, and for this reason is found in certain woods not frequented by the other hole-nesting tits.

(d) Birds dependent on tall trees

A number of species normally nest only in tall trees in the canopy, and hence are absent from woods which do not possess at least one such tall tree. The species primarily concerned are the canopy-nesting Corvidae and Falconidae (set out in Tables 2 and 3). The height of the tree required is rather different for the different species, and also shows local variations in the same species; for instance, on Dartmoor the carrion crow regularly breeds in stunted wind-bent trees, these nests being much lower than in the lowlands a few miles away. The other canopy nesters can be seen from Table 3; most of them require rather lower trees than the Corvidae and Falconidae, each species having a typical minimum height, though most species will nest lower than this in special circumstances.

For other species, tall trees are essential as song posts. Here again, the minimum height varies with the species, and seems rather more rigidly adhered to than in the case of nesting height. The crossbill, tree pipit, blackcap, chiffchaff, mistle thrush, redstart and ring dove may be specially mentioned, but these grade insensibly into species whose minimum height of song post is satisfied in high or low secondary growth. In some of these species, notably tree pipit, blackcap, chiffchaff and redstart, the sole factor essentially supplied by the canopy, and hence by woods, is a tall song post, all the other activities (nesting, feeding, etc.) of these birds occurring predominantly either in the timber, secondary growth, on the ground or in the air. This section is based on the writers' experience. Though observers recorded the height of the trees in their woods, it was not possible from the figures sent in to give any comparative frequency indices for woods of different heights. Too many woods contained trees of variable heights. This aspect is, however, studied in the plantation studies of Schiermann (**12**) and Lack (**4**).

(e) Birds dependent on water

The presence of water brings various aquatic or marsh species into woods—and the grey wagtail then uses trees as song posts, the moorhen for nesting—but such species need not be considered here. One true woodland species, the woodcock, typically breeds near a marsh or stream, by which it feeds. It is interesting that neither trees nor secondary growth are utilized in any of its activities by this predominantly woodland wading bird, which nests in thick ground vegetation and displays in the air. Possibly it gains by the cover afforded by woods, and its rounded wings, unusual in a wader, seem adapted to woods. It does occasionally nest away from woods.

The crossbill usually nests close to water; it seems to drink more than other

birds, perhaps on account of its relatively drier food. The willow tit breeds almost exclusively in damp woods or near water, a habit which it is difficult to correlate with any adaptation or particular activity. Possibly it is connected solely with its need for a nesting hole, which is typically in soft wood excavated by the bird. Such soft, rotten wood is much commoner near water. The species occasionally breeds right away from water, e.g. on the chalk downs (E. M. Nicholson, Venables). The pied flycatcher also occurs regularly along streams, but is by no means confined to such haunts: stream edges provide an open habitat for its "pouncing" feeding habits.

8. Comparison of communities in different woodland types

(*a*) *Broad-leaved deciduous woods, excluding birch*

The typical British oak wood (*Quercus robur* or *sessiliflora*) is only moderately closed, allowing a fair amount of light to penetrate inside the wood. There is usually a slight admixture of other broad-leaved trees, particularly ash (*Fraxinus excelsior*), elm (*Ulmus*) and sycamore (*Acer pseudoplatanus*). (Where the wood also contained conifers, either the count was omitted or, if the conifers were extremely local, the observer omitted that part of the wood from his count.)

There is typically a rich, varied but often patchy secondary growth of deciduous bushes, mainly hazel (*Corylus avellana*), elder (*Sambucus nigra*), hawthorn (*Crataegus*), and saplings of trees, with a few evergreens such as holly (*Ilex aquifolium*), ivy (*Hedera helix*) and *Rhododendron*. There is a varied ground vegetation in which bramble (*Rubus*), bluebell (*Scilla non-scripta*), and bracken (*Pteridium aquilinum*) are conspicuous, together with many other species.

Though most British oak woods are planted, the trees are usually permitted to grow fairly old, hence nesting holes are usually present.

In the recorded counts, nearly all the woods conformed to this type. M 1 to M 5 had many canopy trees of deciduous species other than oak, but were otherwise extremely similar in type, so were included with the oak woods for the indices. H 37 and H 38 were old plantations in which secondary growth was absent. H 39 was oak coppice 18 ft. high, with no secondary growth, no nesting holes and very few forks suitable for nests. H 40 was an extremely isolated wood on Dartmoor, with gnarled stunted trees, no secondary growth, but with rocks and good ground vegetation.

The typical south of England oak or mixed broad-leaved deciduous wood is richer in bird life than any other type of British woodland; but many of the differences between this type and the typical pine woods of Southern England are really correlated with the presence in the former of rich secondary growth, old trees with holes, and comparatively wide spaces between the trees, all of

Phot. H. N. Southern

Phot. 1. Typical oak-mixed broad-leaved wood, showing rich ground vegetation of bracken in foreground and secondary growth of deciduous bushes behind.

Phot. L. S. V. Venables

Phot. 2. Typical older pine plantation, with bare trunks, high canopy and no secondary growth.

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which features are absent from the typical pine plantation. On the edge of Dartmoor are a number of closely planted oak coppice woods, with no secondary growth and no old trees or holes. Here the summer population consists typically of only a few jay, chaffinch, willow and wood warbler, robin and ring dove, which is quite as poor an avifauna as that of the typical older pine plantation (Lack; see also H 39).

The typical oak and mixed broad-leaved wood with good secondary growth contains all the characteristic British woodland species except the few mentioned later as confined to conifer woods or birch. As is very clear from Table 4, the following species breed predominantly in oak and mixed broad-leaved woods and breed at most rarely in pure pine woods even when the latter provide secondary growth (coniferous), nesting holes and open woodland:

Nuthatch	Chiffchaff
Marsh tit	Nightingale
Garden warbler	Spotted flycatcher
Blackcap	Lesser spotted woodpecker
Wood warbler	

Of these species, nuthatch, marsh tit and lesser spotted woodpecker were not recorded breeding in pure coniferous woods at all. However, the last is a scarce bird and does at times frequent coniferous forest in northern Europe (B. W. Tucker). The nuthatch (a different race) also frequents conifer forest in parts of Switzerland (B. W. Tucker). Garden warbler and blackcap occurred occasionally in woods with exclusively coniferous trees but broad-leaved deciduous secondary growth, cases which do not strictly constitute an exception. In addition they occurred rarely in pine woods with no broad-leaved secondary growth on the Norfolk Breckland, as did the chiffchaff and (once) the nightingale (there was one small patch of widely spaced 2 ft. deciduous saplings in the birds' territory). The chiffchaff also breeds occasionally in pure yew scrub (Venables). The wood warbler is scarce but regular in pure pinewoods in Surrey. For the spotted flycatcher the data provided by the enquiry are hardly adequate. It is mainly a bird of the wood edge, but was not recorded from any purely coniferous woods, though it nested on a pine in one mixed wood. However, since it frequents open coniferous woods on the European mainland (B. W. Tucker, F. C. R. Jourdain), its apparent absence from British ones may be due mainly to the scarcity of suitable nesting ledges in the pine plantations of the south of England. One further species, the hawfinch, is typical of broad-leaved woods (oak and beech) and has not been recorded from coniferous woods; it is a secretive species and was recorded too seldom for inclusion in Table 4.

The following additional species typical of oak and mixed broad-leaved woods are regular but definitely much less common (to a varying degree, see Table 4) in pure pine woods:

Bullfinch	Blue tit
Great tit	Green woodpecker

In addition to these, the willow tit (typical of birch woods) breeds regularly in damp oak woods and is absent from pine woods unless these contain stream or marsh side alder or birch stumps. These conclusions are based on data from experienced field observers, not from Table 4, as so many observers cannot distinguish this species from the marsh tit.

The apparent scarcity or absence of the jackdaw and starling from pure coniferous woods is perhaps correlated entirely with the absence of suitable nesting holes in most pine plantations; both nest in pine woods occasionally, hence they were omitted from the above two lists.

The writers have not been able to associate the predominance of the species in these lists in broad-leaved as opposed to coniferous woods with any particular habit or adaptation, except in the case of the nightingale, which builds its nest with dead deciduous leaves. It might be thought that the scarcity of certain warblers in conifers was correlated with the scarcity of secondary growth in English conifer woods, but the Breckland pine plantations provide good secondary growth where some warblers, but not those on these lists, are common. Further, the wood warbler avoids woods with secondary growth, yet is scarce in pine plantations. Alternatively, it might be thought that the scarcity of the warblers in coniferous as compared with broad-leaved woods was correlated with differences in the insect fauna. But all the warblers seem to have an extremely varied insectivorous diet, and here again certain species, but not the others, seem successful in pure pine woods. A further difficulty is that some birds e.g. nuthatch, lesser spotted woodpecker, occur in coniferous woods in other parts of their European range.

(*b*) *Beech woods*

The typical British beech wood (*Fagus sylvaticus*) is moderately closely planted, with a closed high canopy. Secondary growth is typically absent, but is often thick on the edges and in occasional open spaces, and is present (particularly evergreens such as holly, or box (*Buxus sempervirens*) within some woods, though then usually sparse. The woods marked + in the Appendix contained some of such secondary growth, but in nearly all of them much of the wood was devoid of secondary growth. Those marked − had almost no secondary growth at all. Since the trees are usually allowed to reach a considerable age, nesting holes are typically numerous. Ground vegetation is often absent, though there may be moss and sparse grass: the ground is often covered with dead leaves and, in winter, beech mast. All the woods counted were pure or almost pure beech except for J 12, which was predominantly beech but contained some oak and sycamore.

The birds of beech woods with good secondary growth show no diagnostic differences from those of oak and mixed broad-leaved woods, but since in the typical beech plantation secondary growth and ground vegetation are scarce

Phot. H. Rait Kerr

Phot. 1. Typical British beech wood: showing scarcity of ground vegetation and secondary growth. (J 2 of Appendix.)

Phot. 2. Typical Highland birch wood. Trees well spaced, secondary growth of younger birch. (K 17 of Appendix.)

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or absent and holes are specially common, the wood warbler and all hole-nesting species are relatively commoner, and birds dependent on secondary growth are relatively scarcer than in typical oak woods.

(c) *Birch woods*

Typical British birch (*Betula*) woods are found mainly between the north of England and the Scottish Highlands. Those counted were normally open or moderately open, with a deep canopy, and contained fairly old trees and numerous nesting holes. Secondary growth was predominantly birch saplings, with juniper (*Juniperus communis*) in most of the Highland woods, and very occasional gorse (*Ulex europaeus*), hawthorn and elder in various others. The few birch woods counted in the south of England had young trees in close formation, while nesting holes were scarce or absent.

The four mixed birch woods were predominantly birch; L 1 had a few ash and oak, L 2 a number of willows (*Salix*) and rich secondary of the same, and L 3 alders (*Alnus rotundifolia*).

On the whole, the birds of birch woods are similar to those of other broad-leaved types. Three species are specially characteristic of birch woods:

Lesser redpoll	Black grouse
Willow tit	

As shown in Table 4, the lesser redpoll breeds predominantly in birch and in no other wood types; however, it breeds occasionally in pure pine woods, and, especially in gardens in the south of England, nests in many other kinds of trees. The willow tit (whose distribution, as noted, cannot be assessed from Table 4) is typical of birch woods, and is also fairly regular in oak and mixed deciduous woods usually near water. The black grouse is regular in both birch and pine, probably being commoner in the latter; birch is the only type of wood with broad-leaved trees in which it is regular.

Table 4 also shows that certain species are relatively scarcer in birch woods than in other broad-leaved types. This applies to a number of the species which nest in secondary growth. The secondary growth of birch woods is chiefly young birch, and this affords much less suitable nesting sites than typical broad-leaved secondary growth, except for the lesser redpoll, which builds an extremely small nest. It is therefore of interest that one species typical of secondary growth, the willow warbler, is just as common in birch as in typical broad-leaved woods; unlike the other species it is dependent on secondary growth not for nesting (it nests on the ground) but for singing and cover, for which birch seems adequate. From Table 4, jay, nuthatch and green woodpecker would also seem scarcer in birch woods than in other broad-leaved types. This may, however, be a geographical question. Most of the older birch woods counted were too far north for nuthatch and green woodpecker, and the jay

was absent from the region where the Highland counts were taken. If more mature birch woods occurred in the south of England, these three species might be more regular in birch woods.

(*d*) *Other broad-leaved woods*

A few broad-leaved woods of other species were counted. N 1, N 2, N 4, N 5, N 6 and N 8 were young plantations of the species given in the headings, the trees planted close together and secondary growth, where present at all, rather sparse; nesting holes were absent. N 3 and N 7 were old apple (*Pyrus communis*) orchards with widely spaced trees, locally thick secondary growth of hawthorn and willow, and grass below. N 9 was an alder plantation of fairly old trees with a little secondary growth, in marshy ground. O 1, O 2, and O 3 were typical hawthorn scrub.

As is apparent from the Appendix, closely grown young broad-leaved plantations of various species (oak, birch, sweet chestnut (*Castanea sativa*), etc.) are extremely poor in birds; indeed sometimes such plantations have no breeding birds at all. They provide no nesting holes, and, as compared with young pine plantations, the cover and branches are extremely sparse, affording few nesting sites. Apple orchards have, when the trees are old, a fairly rich avifauna, similar to that of parkland. Hawthorn scrub is rich in the birds dependent on secondary growth, but this strictly comes outside the scope of this paper.

(*e*) *Pine woods*

The Scots pine (*Pinus sylvestris*) woods fall into three distinct groups. Those marked H are parts of the natural pine forest still surviving in the Spey valley, in the Scottish Highlands. They consist of old and young trees, well spaced, so that much light gets in, the branches growing to low down on the trees. In A 28, A 29, A 30, A 31, A 48 and A 49 the trees were so far apart that they may be termed "parkland". A 27 differed from the rest of the Highland woods in being a closed plantation with bare trunks. Secondary growth of young pine and juniper was common and well grown in the woods marked + but was absent from those marked −. The undergrowth was mainly thick heather (*Calluna vulgaris* and *Erica cinerea*) and whortleberry (*Vaccinium myrtillus*).

Of the other pine woods, those marked B were closely planted young plantations of 10–20 years old, the essential feature being that the branches still grow down to near the base of the trees. There were no nesting holes and no true secondary growth, but these low branches of the trees are equivalent to secondary growth.

The remaining woods were typical older pine plantations, the trees close together (though thinned out as compared with the B woods), the canopy closed, high and shallow, the trees still so young that nesting holes were very

Phot. 1. Typical young pine plantation before side branches are cut. Dense growth. No other plants. (A 12 of Appendix.)

Phot. 2. Typical Highland pine forest. Trees well spaced, with well developed side branches, good secondary growth of juniper and sapling pine. (A 6 of Appendix.)

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scarce or absent (pines are usually felled much earlier than broad-leaved trees). Typically, there was no secondary growth or ground vegetation, the ground being covered with pine needles. Of the woods containing secondary growth, A 34 had young pines; A 1 birch and young pine; A 4, A 5 and A 17 deciduous secondary growth; A 2 and A 3 holly; and A 10 *Rhododendron*.

For Table 4 two other woods were assessed with the Scots pine woods as they were similar in type. B 1 was Corsican pine (*Pinus nigra Poiretiana*) and contained some deciduous secondary growth; C 1 was a mixed pine and larch plantation.

Table 4 shows that five species breed almost exclusively in coniferous woods:

Siskin	Crested tit
Crossbill	Capercaillie
Goldcrest	

Of these the capercaillie very occasionally nests in pure birch and in pure oak woods; the siskin has bred in alder or birch woods—its winter haunt (also exceptionally in garden trees in the south of England); and the crested tit occasionally breeds in a birch or alder stump, but almost always only in or close to conifer woods. The goldcrest nests regularly, though very sparsely, in pure broad-leaved woods, usually in ivy. In addition to these five species, the blackcock breeds almost exclusively in pine and birch, and the coal tit nests much more numerously in coniferous than broad-leaved woods, though regular and fairly common in the latter. The long-eared owl (as shown by experienced observers' field data, not by Table 4) nests predominantly in pine trees, but is also regular in broad-leaved trees; and one parkland species, the hobby, breeds predominantly but not exclusively in isolated conifers. (From Table 4 the redstart would appear to be commoner in coniferous than broad-leaved woods, but this is not really so. It is a local species and many of the counts of broad-leaved woods were taken outside its range. P 6 (see Appendix) shows how common it can be in broad-leaved woodland—the presence of yews in this wood does not affect it). The species typically absent from and scarce in coniferous woods have already been noted.

The natural pine forests, now surviving in only a few parts of the Highlands (notably the Spey Valley), with their mature trees, open growth and rich secondary growth of young pines and juniper, present such very different conditions from the closely planted pine woods of the rest of Britain that they have been tabulated separately from the rest in Table 4, in which their respective bird populations may be seen. A number of differences depend on the geographical distributions of the species concerned and not on the habitats, northern forms such as hooded crow, siskin, crested tit and capercaillie being recorded only in the Highland forests—also the black grouse, formerly regular but now exterminated in much of England—and southern forms such as the jay, many of the warblers and the green woodpecker being scarce or absent in

the Highlands. If there were mature pine forest in the south of England, it is possible that some of the southern species found in Britain almost exclusively in broad-leaved woods would be commoner in pine woods than at present.

The typical fairly old pine plantation of England is devoid of secondary growth, and hence the species typical of secondary growth are scarce or absent. But many of these species do not avoid pine woods as such; a number of them, notably whitethroat, willow warbler, song thrush, robin, dunnock and wren, occur commonly in pure young pine plantations before the bottom branches disappear. (For further details concerning the fauna of young plantations see Lack (**5**), Schiermann (**12**) and the woods marked B in the tabulated counts in the Appendix.)

Of the predominantly coniferous species, the crossbill feeds almost exclusively on pine cones, the capercaillie (especially in winter) on pine shoots. The other species are more varied in their food, and it is difficult to associate their predominance in conifers with any particular habits or adaptations, except that the goldcrest is clearly restricted (though not absolutely) by its nesting site, since it is common in broad-leaved woods provided there is one coniferous tree in which to nest, but when conifers are quite absent it is scarce (see later discussion).

(*f*) *Larch woods*

Larch (*Larix europaeus*) woods are not very common in England, and only a few were investigated. These were closed, fairly young plantations with a high canopy, usually deeper than in Scots pine plantations. Broad-leaved secondary growth was present in those marked +. Typically, undergrowth and nesting holes were absent.

The avifauna of larch plantations closely resembles that of pine plantations, but some of the species characteristic of broad-leaved woods and rare or absent in pine woods seemed appreciably commoner in larch, notably great, blue and marsh tits, and perhaps song thrush, also jay. It should, however, be emphasized that the number of larch woods counted is too small for safe generalizations. (Some of the most characteristic pine-wood species—crossbill, siskin, crested tit and capercaillie—were not recorded from larch woods in the present enquiry; but no Highland larch woods were counted. The Scottish crossbill breeds regularly in larch and the siskin occasionally (F. C. R. Jourdain).

(*g*) *Other coniferous woods*

A few other coniferous woods (see Appendix) were counted, but too few for any generalizations concerning their bird life. The three spruce (*Picea*) plantations were very similar to Scots pine, but the canopy was denser and deeper; E 1 had secondary growth of birch, rowan (*Pyrus aucuparia*) and *Rhododendron*. The juniper and the yew woods were on chalk grassland, the trees up to 10 ft. in height, in some parts dense, in others open. The juniper

wood is similar to a young pine plantation; the yew wood has numerous holes—hence the abundance of tits and robins. G1 was a very mixed conifer plantation, chiefly of young trees.

(*h*) *Mixed broad-leaved and coniferous woods*

P 1 was mixed pine, birch, oak and holly with a little deciduous secondary growth; P 2 was a coppice with oak predominating, but with many other deciduous trees and some pine, a little secondary growth and much ivy; P 3 was a park, the trees, spaced at intervals, chiefly consisting of mature oak, with some other deciduous trees and with a few pine and spruce, locally a little secondary growth. P 4 and P 5 were closely planted, with no secondary growth, the former mainly Scots pine with some oak, the latter mainly beech with some Scots pine.

Counts were done in a few mixed woods. As can be seen, mixed woods may have a richer avifauna than any other British woods. This is to be expected, since they can provide all possible combinations of requirements. P 4 and P 5 show the effects of absence of secondary growth. P 3 was included to show the birds characteristic of a country park. P 6 is a typical broad-leaved wood, except for the presence of yews, which bring in the goldcrest. The yew was presumably present in the natural oak forests of England.

9. WINTER DISTRIBUTIONS

Winter counts were taken between November and February. The habitat distributions of the different species in the various types of woods are mostly similar to those of the breeding season. In this section the more important differences as compared with summer distributions will be mentioned.

Since this paper is not primarily concerned with geographical distributions, the disappearance of a number of migratory woodland species from Britain (which is apparent from Table 4) need have no more than passing mention. A number of other birds, such as the Turdidae, are partial migrants. Three winter visitors to Britain frequent woods: the brambling being the commonest, the redwing being regular for roosting but feeding chiefly in the open country, and the fieldfare, which is, like the redwing, characteristic of fields and hedgerows, occurring at times.

In winter, the hole-nesting species and those which require tall song posts are no longer dependent on these features, and hence are more widely distributed than in summer. The appearance of tits and woodpeckers in winter in young plantations, where they cannot breed in summer owing to the absence of nesting holes, may be specially noted. Also secondary growth, especially if deciduous, is a much less important factor in distribution than in summer.

All species of tits, with the goldcrest, nuthatch, tree creeper and an occa-

sional great and lesser spotted woodpecker, tend to form into mixed foraging parties which wander through the woods. They make their way from one wood to another along hedgerows, through gardens, etc., rarely taking long flights in the open. Hence such species are rare in extremely isolated woods, such as Wistman's Wood (H 40) on Dartmoor, which is well over a mile from any other cover. Another mixed group which often feed together in winter are the lesser redpoll, siskin, goldfinch and the tits of the genus *Parus*, this group being characteristic of birch and alder woods. Unlike the members of the first group, redpoll, siskin and goldfinch will take big flights across the open. The goldfinch was excluded as a true woodland bird and placed in Table 1, as it is much more characteristic of open country than woods when breeding; in winter, however, it is regular in woods of all types, the same applying to the greenfinch.

The roosting place is a very important factor in winter distributions, but, as already noted, it was not studied in the present paper. It may be noted that quite a number of species which feed primarily in the open country frequent woods in winter for roosting. This subject forms a wide gap in present knowledge of the bird ecology of woodlands.

As is apparent from Table 4, the most marked differences in habitat distribution between winter and the breeding season are as follows:

(1) The siskin, which breeds almost exclusively in conifers, is in midwinter found almost exclusively in birch and alder. (In the early spring it again returns to larch and pine.)

(2) Most chaffinches leave the coniferous woods, the birch, and to a rather less extent the oak woods. They form huge flocks feeding in beech woods on the beech mast, and many others frequent the open country.

(3) The brambling, which breeds in the Scandinavian birch and pine woods, visits Britain in winter. In midwinter in woods it is almost confined to beech woods, joining the chaffinch flocks in feeding on the beech mast, but it is very occasional in other woodland types, and is regular in open country. (In early spring it frequents birch and pine.)

(4) The goldcrest, while still very abundant in conifers, is quite regular in smaller numbers in oak, mixed broad-leaved and birch woods.

(5) A number of species such as carrion and hooded crows, rook, jackdaw and starling, which occur in woods in the breeding season primarily because of nesting sites, tend to leave the woods in winter for the open country, though they often return to the woods in the evenings for roosting,—rook, jackdaw, starling (and also ring dove) roosting in large flocks.

(6) Many mistle and song thrushes leave the woods for the open country after the disappearance of the autumn berries.

(7) The long-tailed tit, which in the breeding season is found mainly in secondary growth, in winter wanders through all types of woods much more commonly, and is regular in the canopy.

(8) Nearly all birds wander from wood to wood much more in winter than

in summer, hence there is a much greater tendency for species which occur almost exclusively in one type of wood to straggle into another, e.g. lesser redpolls occasionally occur in all the main types of woods, though typical of birch only (also pine in early spring); and the nuthatch, which is typically confined to broad-leaved woods, is very occasional in pure conifers.

10. Distributions at other seasons

Distributions of woodland birds at seasons other than the breeding season and midwinter were not studied in this enquiry, so only a few brief and incomplete notes are given here. It should be specially noted that the change-over from the breeding to the winter type of distribution occurs in many species immediately after they have nested, in the middle of the summer, and in some cases before other species of woodland birds have finished breeding. Thus already in late June some of the tit and goldcrest parties have formed and wander into habitats not frequented in the spring, and in late summer and early autumn a number of the warblers and the spotted flycatcher join up with these foraging parties, feeding on the insects disturbed by the tits.

When caterpillars, notably of *Tortrix*, swarm in late summer, there is an influx of many species to the woods to feed on them, including rook, starling and many smaller birds. The rowan and other autumn berries bring an influx into the woods of various species, particularly the Turdidae, including the ring ouzel, a passage migrant from the moors. Ring doves are common in oak woods when the acorns fall, and also invade the Dartmoor oak woods when the whortleberries (*Vaccinium myrtillus*) ripen. In the early spring some of the winter visitors from the north, notably brambling, lesser redpoll and siskin, move from their winter to their summer habitat, as noted in the last section. Some movement goes on among woodland birds even in the middle of the breeding season, for the pure oak coppice woods on the edge of Dartmoor are almost devoid of birds until the leaves appear in mid-May, after which there is a marked influx of chaffinch, robin, wood warbler and a few other species (Lack). In both spring and autumn, migrant birds on passage stop for a while in woods of types sometimes unfrequented by them at other seasons, but these occurrences are not of sufficient ecological importance for detailed reference.

The above notes are extremely incomplete, but are sufficient to show that the bird population of woods is far from static at any season.

11. Comparison with the North European mainland

Palmgren (**9**, **10**, **11**) has made most valuable and detailed studies of habitat distribution in the woods of south Finland, and when similar studies have been made in the rest of Europe, some very interesting comparisons

will emerge. Schiermann (**12**) gives habitat data from north Germany and Sundström (**14**) from Finland; but for the rest of Europe the data are almost confined to general avifaunal studies, notably by Niethammer (**8**).

Comparison with Palmgren's data in particular shows many striking similarities in the habitat distributions of the various woodland species, even when these refer to different geographical subspecies. For instance, in south Finland great and blue tits (different subspecies from the British races) are mainly in broad-leaved woods, but regular, though very uncommon, in pure coniferous woods—just as they are in Britain. There is no need to comment specially on the many other points of similarity. The large number of British woodland birds which are represented by different subspecies from the Continental forms indicates that the British woodland avifauna has been isolated from that of the Continent for a long time, but nevertheless the habitat distributions have remained nearly the same.

As regards the differences in distribution between south Finland and Britain some, such as the predominance in south Finland of jay, bullfinch, mistle thrush, song thrush, robin, wren and ring dove in coniferous woods (some in spruce, some in pine) as opposed to broad-leaved woods, are perhaps not correlated directly with the species of trees, but with other local conditions, since these birds show no such tendency in Britain, where a much greater variety of broad-leaved woodland types are afforded than Palmgren could investigate in south Finland. Some further differences are detailed below.

Tree creeper: Palmgren notes *Certhia f. familiaris* (L.) as restricted to conifers. Stresemann (**13**) in a general survey states that this is true of much of its range, but that in parts of its European range it occurs in broad-leaved woods. The British race, *C. f. brittanica* Ridgw., seems quite as common in broad-leaved as coniferous woods. Incidentally the American form (*C. f. americana* Bp.) is by no means restricted to conifers.

Goldcrest: Palmgren notes *Regulus r. regulus* (L.) as confined to conifers, and this is supported by other Continental authorities. In Britain it is a sparse, but quite regular, breeding species in pure broad-leaved woods, and is quite common there in winter.

Coal tit: Parus a. ater L. would also seem to be nearly confined to conifers, though not entirely. The British race is common in broad-leaved woods, though not so abundant as in conifers.

Willow tit: Parus atricapillus borealis Selys-Longchamps, is regular in south Finland, not only in broad-leaved woods, but also in pure coniferous woods, a habitat in which the British race was not recorded breeding unless a birch or alder stump was present.

Chiffchaff: Schiermann records *Phylloscopus c. collybita* (Vieill.) as regular in pine plantations, and in south Finland Palmgren records *P. c. abietinus* (Nilss.) as true to spruce. In the present British enquiry, almost no chiffchaffs were recorded from pure coniferous woods.

Lesser whitethroat: Both Palmgren and Schiermann record this bird as typical of coniferous scrub, whereas in England it is almost always in broad-leaved deciduous scrub.

12. Historical considerations

Any consideration of present habitat distributions must eventually take into account the distributions in the past, though knowledge of the latter is necessarily speculative. It seems probable that after the last Glacial Period there was a period when even the south of Britain was covered with conifer and birch forest, which presumably contained only the birds characteristic of these woods, such as crossbill, siskin, lesser redpoll, tree creeper, goldcrest, coal tit, willow tit, crested tit, capercaillie and black grouse. Gradually the conifer-birch belt must have moved northwards, to be replaced in the south by mixed oak forest, and with this change some of the more southern birds characteristic of oak woodland, such as marsh tit, nuthatch, nightingale, lesser spotted woodpecker and green woodpecker—presumably colonized the country. At the same time, many of the birds of the conifer-birch forest presumably retreated northwards, amongst them crested tit, siskin and Scottish crossbill. But other species, especially the tree creeper and coal tit, and to a less extent the goldcrest, would seem to have spread into the oak woodland with success. As regards the goldcrest, it breeds only sparsely, though regularly, in pure oak woods, but it was probably much commoner in the natural oak forests of England than this suggests, for it readily breeds in isolated yew trees even when all the other trees are broad-leaved. For instance, it is common in the New Forest in woods containing purely broad-leaved trees except for yews (P 6 in the Appendix is a typical population for this type of woodland). Yews were presumably present in the natural oak forest. Hence the goldcrest has adapted itself less than tree creeper or coal tit, but sufficiently for it to be regular in natural oak forest.

In addition to these natural changes in the forest conditions, man has caused drastic changes. Except for some natural pine forest in the Scottish Highlands, almost no extensive original forest survives in Britain to-day. Planted woodlands cover a far smaller area than the original forests did, hence possibly the Corvidae and some other birds were once much less frequent outside woods than they are to-day. Further, the conditions in a planted wood are different from those of natural forest. Oak and mixed broad-leaved planted woods are often permitted to grow for so long that they simulate small areas of natural broad-leaved forest (except with regard to the frequent absence of yews, which affects the goldcrest); but coniferous plantations are usually cut long before they approach the conditions of natural forest. Plantations are usually closely planted and have little or no secondary growth, and are often

so young that nesting holes are absent. Hence they afford much less suitable conditions than does natural forest for many woodland birds.

Man has further upset the natural conditions by introducing types of trees not naturally found in the area concerned. Various species of trees foreign to Britain have been introduced, most only as isolated trees, but some, and in particular the larch, in extensive plantations. Of particular interest, especially during the last hundred years, Scots pine has been reintroduced on a large scale in much of southern and eastern England. It is interesting to compare the birds of these new southern pinewood areas with those of the natural pine forest in Scotland, the latter presumably resembling the avifauna of southern England at an earlier time. As might be expected, the three characteristic coniferous species which have successfully colonized the southern oak woodland, namely coal tit, tree creeper and goldcrest, have colonized these new pinewood areas. (The present scarcity of the tree creeper can be correlated with the scarcity of old trees suitable for its nesting cracks in the new plantations.) But the other coniferous species, such as siskin and crested tit, now restricted to the north of Britain, have failed to colonize. It is of special interest that, although another member of this latter group, the Scottish crossbill, has also failed to colonize, the Continental race of this bird (*L. c. curvirostra* L.), which periodically irrupts into England, has now established itself in these southern pinewood areas.

13. Factors influencing habitat distribution

A species may be limited in its habitat distribution by various factors: food (e.g. crossbill), feeding habit (flycatchers), song post (blackcap), nesting site (hole-nesters), nest material (nightingale), and roosting place (pheasant). Further examples of these types will be found in the text, and Palmgren (**10**) may be referred to for admirable examples, worked out in detail, of nesting restrictions. It should be emphasized that though these habits are *associated* with the limitations concerned, it does not follow that they are the *cause* of the limitations. In many other cases, the limitations cannot be correlated with any known habits or adaptations, and though in some cases this may be due to the inadequacy of present knowledge, it seems probable that in many cases such associated habits and adaptations do not exist.

A further difficulty in accounting for the restrictions of certain birds to woods of a particular kind of tree is that, in nearly all such cases, the bird does occasionally breed in other wood types. For instance, both goldcrest and capercaillie, typically confined to conifers, occasionally breed in oak woods, and the nightingale, typical of broad-leaved woods, has bred in pure conifers. Other examples were given earlier. In other cases the species is typical of one wood type, but is regular in very much smaller numbers in another type; for instance blue and great tits are typical of broad-leaved woods, but regular,

though much less common, in pine woods. There is a gradation through species like the coal tit, which to judge from its frequency index is rather more than twice as common in conifers as in broad-leaved woods for breeding, to species like the chaffinch which is almost equally common in all types of woods.

The distribution of the black grouse, which is regular in both pine and birch, but not in other broad-leaved types, is particularly difficult to understand, since no environmental factor common to pine and birch, but lacking in the other broad-leaved types, is apparent in a study of either the woods concerned or of the habits of this bird. Another interesting point is that the British tree creeper and British coal tit seem to breed much more frequently in broad-leaved woods than do the Continental subspecies of these birds.

In their inability to interpret most of the observed habitat restrictions and limitations to distribution, the writers find themselves in much the same position as Lack (**4**) on the Breckland, and Moreau (**7**) in the Usambara forests. It seems that, while some limitations are correlated directly with particular environmental factors or with structural adaptations, these cannot account for all cases, and that habitat selection is determined in part by factors on a psychological plane, the significance of which is connected with the past history of the species. (Some general aspects of the psychological factor in habitat selection are discussed by Lack (**6**); the following discussion should be considered an addition to this review.)

It may be tentatively suggested that the greater frequency in broad-leaved woods of the British tree creeper, coal tit and goldcrest than the Continental subspecies of these same birds, may be due to a psychological rather than a structural adaptation. (If any structural adaptation is present it must be extremely inconspicuous.) Again, it may be a limitation of habit rather than of structure which restricts the black grouse to pine and birch, perhaps because of this species being originally a northern bird for which the only available wood types would be conifers and birch. The latter habitats may be instinctively selected, while the other broad-leaved wood types are not, although the latter (due especially to human planting) are now within the black grouse's geographical range and are perhaps not otherwise unsuitable.

One of the most puzzling features of British woodland bird distributions is this restriction of certain species to conifer, to birch or to oak broad-leaved woods. As already noted, these restrictions could not, in most instances at least, be correlated with any structural adaptations or particular habits. In many cases, however, they can be correlated with one factor, namely geographical distribution. Of the eight species classified as typical of pine or birch, seven (siskin, lesser redpoll, Scottish crossbill, crested tit, willow tit, capercaillie and black grouse, i.e. all save goldcrest) are predominantly, and some exclusively, northern birds in Britain to-day. On the other hand, of the ten species typical of oak-woodland six (hawfinch, nuthatch, marsh tit, chiffchaff, nightingale and lesser spotted woodpecker) have definitely southern

distributions (possibly blackcap, garden warbler and wood warbler could be added), and so has the green woodpecker (from the list of four additional predominantly broad-leaved woodland species).

This correlation is far too striking to be due to chance, and with the apparent absence of other correlated factors we may seek in geographical distributions for an explanation of the habitat restrictions. What is the significance of the correlation? Certainly the limit to the geographical distributions of the birds is not caused by adherence to a type of tree which is geographically restricted. Thus nuthatch, marsh tit, nightingale and the rest disappear towards the north long before broad-leaved woodland becomes scarce. Similarly, siskin, crested tit, etc., disappear or become scarce in the south where coniferous plantations are common. On present evidence, the most probable explanation seems to be along the lines already suggested for the black grouse that a number of southern species (not, of course, all) tend to frequent oak broad-leaved woodland, and a number of northern species tend to frequent pine and/or birch, simply because these were the habitats originally available to the species in question, and the inherited habits of these species are now such that they tend to select the ancestral habitat even when, as in Britain to-day, other habitats, quite possibly suitable, have become available.

A further characteristic of these habitat restrictions is that an exceptional break-away from the restriction has been recorded in Britain for nearly every species concerned, and for the remainder on the European mainland; the existence of such exceptions is much easier to account for if the restrictions are primarily due to habit and not to structural adaptation. It is not intended to rule out the possibility of structural adaptations being involved in some cases, though if such exist it seems quite probable that the structural adaptation was evolved subsequently to the habit; however, it may be pointed out that adaptive structural differences are more characteristic as between different genera of birds than as between different species of the same genus, and in the distributions under discussion one may find only one species out of several in the genus showing the restriction in question (cf. tits), or even only some, and not all, of the subspecies of one species (cf. goldcrest, chiffchaff). The general considerations of the nature of bird behaviour which make such restrictions of habit, and so of habitat, not only possible, but likely, have already been discussed by Lack (**6**).

14. The woodland bird community

In previous sections the niches in woods filled by the various woodland birds have been described and to some extent discussed. The interrelations of woodland species cannot be adequately described without quantitative study, which was not an object of the present enquiry, but a few points may be briefly mentioned.

There is competition for nesting holes among certain species, but in most

species competition for nesting sites is entirely absent. Some species, e.g. hobby, tend to use the nests of other species. Various species eat the same sorts of food, but there is no definite evidence as yet as to whether, and to what extent, one species significantly affects another as a result of this. A few species of birds prey on the adults, or eggs and young, of others. Territorial behaviour perhaps affects the density of individuals within a species, but there is very little evidence of one territorial species thereby affecting the density of another. The foraging parties outside the breeding season perhaps result in mutual benefit, one species disturbing insects which are thus rendered available for another. In these and other ways, the various woodland species interact, but the general impression gained is that the woodland bird "community" is extremely loosely knit: most of the species are by no means confined to woods, many seem quite independent of any other bird species, and in many others the interaction is extremely slight—from the standpoint of population density perhaps negligible. The various woodland birds occur in woods correlated with widely different features in different cases. Vegetational factors, and not other bird species, are primarily responsible for their occurrence side by side, and the birds interact with each other to a far smaller extent than the members of a plant community.

15. SUMMARY

1. A co-operative survey was organized under the auspices of the British Trust for Ornithology, in the course of which 152 woods were investigated in summer and 120 in winter. Fifty-seven individuals and organizations took part in the survey.

2. The requirements of British woodland birds are summarized in Tables 1–3, and a comparative index of their abundance in different types of wood is given in Table 4. The full data are contained in an Appendix.

3. Some species are limited to open as opposed to close woods, others are limited by secondary growth, nesting holes, tall trees (as nests or song posts), and a few by water.

4. Both mixed broad-leaved woods and natural pine forest are rich in birds, but plantations of both are poor, correlated with close planting and scarcity of holes and secondary growth.

5. Eleven species of birds are almost confined to broad-leaved as opposed to coniferous woods (two of these being characteristic of birch), and five to coniferous as opposed to broad-leaved woods. A few species are abundant in all the main types of woods.

6. The winter habitat distributions are mainly similar to those of the breeding season, the exceptions being discussed.

7. Comparison with the north European mainland shows that most habitat distributions and limitations are the same, with some exceptions that are mentioned.

8. Some habitat limitations can be associated with particular habits or adaptations, but this does not necessarily mean that the latter are responsible for the limitations. For the most part, such associated habits or adaptations have not been found. But the restriction of certain species to conifers or birch or both, and of others to oak woodland could definitely be correlated with geographical distribution, the former being mainly northern and the latter southern species. It is tentatively suggested that this is correlated primarily with habitat limitations on a psychological plane associated with the past history of the species.

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																				Oak													
Locality	...	S.E.	S.E.	S.E.	M.	M.	C.	N.	S.E.	E.	S.E.	M.	C.	C.	C.	C.	C.	C.	C.	C.	C.	C.	M.	C.	C.	C.	M.	M.	Sc.	C.	S.E.	S.E.	S
Secondary	...	+	+	+	+	½	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	½	½	+	+	+	+	
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Reference no.	..	H 1	H 2	H 3	H 4	H 5	H 6	H 7	H 8	H 9	H 10	H 11	H 12	H 13	H 14	H 15	H 16	H 17	H 18	H 19	H 20	H 21	H 22	H 23	H 24	H 25	H 26	H 27	H 28	H 29	H 30	H 31	H
Carrion crow		.	.	2	.	2	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	.	1	.	.		
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Starling		2	.	3	.	3	4	.	4	.	.	40	.	.	2	.	1	2	2	3	.	.	.	.	.	.	.	4	.	1	.	4		
Greenfinch		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
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Chaffinch		1	.	3	2	6	6	15	9	4	3	2	.	2	3	4	6	4	2	14	.	7	4	2	6	2	3	10	5	4	2	4		
Brambling		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
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Crossbill		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Yellow bunting		.	.	.	.	.	.	.	1	.	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.		
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Nuthatch		1	1	3	.	.	2	.	1	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	.		
Goldcrest		.	.	.	.	.	1	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Great tit		2	1	5	2	.	7	10	4	2	1	3	1	.	.	1	1	2	.	3	.	2	4	.	2	4	.	.	5	2	.	.		
Coal tit		1	1	1	.	.	3	4	.	1	.	4	.	.	.	1	.	2	.	1	.	2	4	.	.	2	2	.	5	2	.	.		
Marsh tit }		1	2	1	.	.	7	.	4	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Willow tit }		.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	1	.	.	.	4	.	6	2	.	.	.	1	.	.		
Blue tit		4	.	7	4	8	10	16	5	4	.	2	1	2	3	2	3	1	6	4	.	.	6	1	1	2	.	.	10	4	.	.		
Long-tailed tit		2	2	2	.	.	5	2	2	.	.	.	.	.	.	.	.	.	.	4	.	2	2	1	3	.	1	.	.	4	.	.		
Whitethroat		2	.	.	.	2	2	.	.	.	1	4	1	.	2	1	1	4	2	2	.	3	1	.	.	2	.	.	.	8	.	.		
Lesser whitethroat		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	1	.	1	1	.	.	.	.	.	.	.		
Garden warbler		.	.	.	.	.	2	.	.	.	1	4	.	.	2	.	4	3	.	.	.	.	2	.	.	.	.	.	.	4	.	.		
Blackcap		1	.	1	.	.	3	.	.	.	1	3	.	.	2	.	4	2	1	4	.	.	2	.	1	.	.	.	.	6	.	.		
Willow warbler		2	.	1	1	1	3	14	2	.	2	5	4	5	5	2	7	3	6	12	4	10	6	7	7	2	3	.	3	6	2	2		
Wood warbler		.	.	.	.	.	.	.	1	1	.	2	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.		
Chiffchaff		2	1	.	.	6	3	.	1	2	.	1	.	.	.	.	5	.	1	7	1	3	6	2	2	.	2	1	.	6	.	.		
Mistle thrush		1	.	1	2	4	.	.	3	2	3	3	.	1	2	2	2	.	1	.	1	.	2	.	.	.	.	.	.	.	.	.		
Song thrush		1	.	1	.	7	1	7	3	7	.	6	2	2	2	4	1	4	3	4	1	.	2	4	3	1	2	1	3	6	.	1		
Redwing		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
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Robin		1	.	1	3	6	7	.	1	5	3	2	3	1	2	3	6	6	3	7	5	7	14	7	5	1	4	4	5	6	1	1		
Nightingale		.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	1	.	.	.	1	7	.	.	.	.	4	.	.		
Dunnock		1	.	.	.	.	1	4	.	.	.	1	.	1	1	.	1	1	.	1	1	.	1	.	.	2	.	.	.	1	1	.		
Wren		5	2	1	1	6	6	4	1	1	1	1	.	2	1	1	2	1	1	6	.	3	7	2	4	2	.	.	10	4	2	2		
Spotted flycatcher		.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Great spotted woodpecker		1	.	1	.	.	2	2	.	.	.	3	.	1	.	1	1	.	.	1	.	.	3	.	.	1	.	.	.	1	.	.		
Lesser spotted woodpecker		.	.	1	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	1		
Green woodpecker		.	.	2	2	.	1	.	1	.	1	2	.	.	.	.	.	.	.	2	.	1	2	.	.	.	.	.	.	1	.	.		
Wryneck		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Cuckoo		2	.	.	.	.	.	.	1	1	.	1	.	.	1	.	1	3	1	5	.	2	2	2	.	.	.	1	.	1	.	.		
Barn owl		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Tawny owl		.	.	.	.	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.		
Little owl		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Buzzard		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Sparrow hawk		.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.		
Kestrel		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	1	.	.	.	.	.	.	1	.	.		
Heron		.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Woodcock		.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Stock dove		.	.	1	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Ring dove		.	.	30	5	6	5	7	1	.	1	2	8	4	6	5	11	.	3	7	1	4	7	2	.	8	.	40	.	2	.	.		
Turtle dove		.	.	.	.	2	.	.	.	.	.	.	1	2	2	.	2	.	.	.	.	.	.	.	.	.	.	.	.	2	.	.		
Pheasant		2	.	.	.	.	2	.	.	2	3	.	.	.	.	.	7	2	2	11	.	13	1	.	6	.	.	1	.	.	.	.		
Capercaillie		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Black grouse		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		

		Oak																																	
Locality ...		S.E.	S.E.	S.E.	E.	M.	C.	C.	C.	C.	C.	C.	C.	C.	C.	C.	M.	C.	C.	C.	C.	C.	C.	C.	C.	S.E.	E.	E.	C.	S.E.	S.E.	S.W.	S.W.
Secondary ...		+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
Number of counts ...		2	1	2	4	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	8	1	1	1	1	1	1	2	2		
Reference no. ...		H 2	H 1	H 3	H 9	H 11	H 13	H 12	H 14	H 15	H 16	H 17	H 18	H 19	H 20	H 21	H 22	H 23	H 24	H 25	H 41	H 42	H 43	H 44	H 45	H 46	H 47	H 48	H 49	H 50	H 51	H 52	H 53		
Carrion crow		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	3	.	2	.	.	.	.	.	.	.	.	1	.		
Hooded crow		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Rook		.	.	.	.	.	.	.	.	1	7	5	7	5	2	3	.	.	5	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Jackdaw		.	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	2	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Magpie		.	.	1	.	2	.	.	.	.	.	.	.	2	1	2	.	1	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Jay		.	1	.	9	2	.	.	.	.	4	6	.	4	2	8	1	1	29	.	.	1	1	1	5	13	.	4	2	2	4	3	1		
Starling		.	.	.	.	1	.	.	.	.	.	.	.	.	.	1	.	.	7	.	.	.	.	.	2	8	.	.	.	.	.	.	.		
Greenfinch		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Hawfinch		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	6		
Goldfinch		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.		
Siskin		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
House sparrow		.	.	.	.	.	.	.	3	.	2	.	4	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Tree sparrow		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Chaffinch		.	.	.	4	.	.	1	2	4	5	6	15	.	1	.	.	6	.	.	.	.	.	4	1	8	.	.	.	.	2	.		
Brambling		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Linnet		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Lesser redpoll		.	.	.	.	.	15	.	.	.	.	.	.	.	.	.	.	.	.	.	12	.	.	.	16	.	.	.	.	.	.	.	.		
Bullfinch		.	.	.	2	4	.	.	.	.	.	.	.	4	.	3	1	.	1	2	.	.	.	.	11	.	6	.	.	.	.	.	.		
Crossbill		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Yellow bunting		.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Cirl bunting		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Woodlark		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Tree pipit		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Tree creeper		.	1	.	1	1	.	.	.	.	.	.	.	.	.	.	2	.	.	1	1	.	.	2	1	.	1	1	1	.	.	2	1		
Nuthatch		1	1	2	6	.	.	.	.	.	.	.	2	.	.	.	.	.	.	1	.	.	.	.	2	.	.	3	.	1	1	2	4		
Goldcrest		2	1	.	.	2	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	2	3	.	1	.	2	2	5	10	3		
Great tit		1	.	1	4	4	.	.	2	.	6	3	4	19	.	13	4	.	8	1	1	1	2	.	6	7	3	.	3	2	1	1	1		
Coal tit		.	1	.	.	1	.	1	.	1	2	3	7	.	1	1	.	.	2	2	2	1	.	.	3	2	3	1	.	4	1	3	1		
Marsh tit }		1	4	2	2	1	.	.	1	7	.	.	2	3	1	2	3	.	.	23	.	.	1	.	4	3	7	11	2	2	4	2	3		
Willow tit }		.	.	.	.	1	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	2	.	.	.	.	.	.	.		
Blue tit		1	.	3	.	7	3	.	3	2	11	12	14	10	2	13	9	.	30	1	5	.	.	.	15	11	9	5	5	5	8	11	7		
Crested tit		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Long-tailed tit		6	.	6	.	5	.	.	2	.	12	4	1	17	6	7	.	.	14	7	4	.	.	.	12	27	10	.	7	.	8	5	3		
Whitethroat		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Lesser whitethroat		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Garden warbler		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Blackcap		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Willow warbler		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Wood warbler		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Chiffchaff		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Mistle thrush		.	.	.	1	.	.	.	.	1	.	1	.	.	.	1	.	.	.	.	4	.	.	.	2	.	.	1	.	.	.	.	.		
Song thrush		.	.	.	.	.	.	1	1	.	7	2	3	4	1	12	.	1	1	.	1	1	2	3	2	.	.	1	1	.	.	.	.		
Redwing		.	.	.	8	1	.	.	.	.	.	.	.	.	.	.	12	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.		
Fieldfare		.	.	.	.	.	.	.	.	.	.	.	.	.	.	2	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Blackbird		1	1	1	13	8	.	9	14	13	21	7	14	62	3	32	10	8	70	1	6	1	3	7	12	1	3	8	4	.	1	3	.		
Redstart		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Robin		2	.	.	5	.	2	.	.	5	13	5	5	24	2	20	.	2	13	3	3	2	3	2	5	.	2	2	6	3	5	4	3		
Nightingale		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Dunnock		.	.	1	2	.	.	.	.	.	.	.	.	3	1	3	.	2	2	.	5	.	2	.	4	.	7	.	.	.	2	1	.		
Wren		.	7	2	2	2	.	.	.	.	.	.	3	1	1	2	2	.	3	.	2	1	.	.	6	.	4	4	6	1	5	7	5		
Spotted flycatcher		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Great spotted woodpecker		.	1	.	.	.	.	.	.	.	.	.	.	.	1	2	.	.	.	.	.	.	.	.	1	4	.	1	.	.	.	1	.		
Lesser spotted woodpecker		1	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.		
Green woodpecker		.	1	.	.	.	.	.	.	.	2	1	.	1	.	7	1	.	.	.	.	.	.	1	2	.	.	.	.	.	.	.	.		
Wryneck		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Cuckoo		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Barn owl		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Tawny owl		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Little owl		.	.	.	.	.	.	.	.	.	.	.	1	6	1	.	.	.	2	.	.	.	2	1	.	.	.	.	.	.	1	.	.		
Buzzard		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1		
Sparrow hawk		.	.	.	.	1	.	.	.	.	.	.	.	3	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.		
Kestrel		.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.		
Heron		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Woodcock		3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.		
Stock dove		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Ring dove		.	.	10	95	7	3	.	16	5	16	1	2	.	.	5	.	.	3	.	43	2	.	1	1	.	5	4	23	.	3	4	2		
Turtle dove		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Pheasant		1	.	.	.	.	.	2	.	.	1	2	3	7	1	15	1	1	35	.	1	.	2	.	.	.	6	8	.	.	.	.	.		
Capercaillie		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		
Black grouse		.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.		

Scots pine

Locality ...	S.E.	S.W.	S.W.	C.	H.	S.E.	S.E.	E.	E.	C.	E.	E.	S.E.	S.E.	Sc.	Sc.	C.	S.E.	E.	E.	E.	E.	E.	E.	E.	E.
Secondary ...	½	+	+	+	+	+	B	B	B	B	B	B	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Number of counts ...	12	1	1	1	2	1	2	1	1	1	1	1	2	2	1	1	1	1	1	1	1	1	1	1	1	1
Reference no. ...	A 1	A 2	A 3	A 5	A 33	A 34	A 11	A 12	A 13	A 35	A 36	A 37	A 16	A 17	A 22*a*	A 22*b*	A 26	A 38	A 39	A 40	A 41	A 42	A 43	A 44	A 45	A 46
Carrion crow	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hooded crow	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Rook	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Jackdaw	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Magpie	3	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Jay	2	.	.	.	.	.	1	1	1	1	.	.	.	1	.	.	1	1	2	.	.	.	.	.	1	.
Starling	.	.	.	3	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Greenfinch	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hawfinch	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Goldfinch	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Siskin	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
House sparrow	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Tree sparrow	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Chaffinch	1	.	1	3	.	1	.	.	1	.	1	3	.	.	.	.	.	.	1	.	.	.	.	.	.	.
Brambling	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Linnet	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lesser redpoll	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Bullfinch	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Crossbill	4	.	.	.	.	.	2	.	.	.	2	2	10	.	.	.	.	.	.	.	.	.	.	.	.	.
Yellow bunting	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cirl bunting	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Woodlark	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Tree pipit	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Tree creeper	.	1	.	.	.	.	1	.	1	.	.	.	1	1	4	10	.	.	.	3	.	.	.	2	2	.
Nuthatch	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Goldcrest	5	3	5	.	20	2	10	15	49	.	4	4	5	2	10	37	.	2	3	2	4	4	4	3	5	4
Great tit	.	.	.	2	.	1	1	.	.	.	.	.	.	.	.	.	2	.	.	.	.	.	.	.	.	.
Coal tit	7	6	4	4	20	2	9	12	38	.	2	4	5	2	5	13	9	5	2	2	3	2	2	1	5	2
Marsh tit }	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Willow tit }	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Blue tit	2	.	.	.	.	.	6	3	9	1	.	.	6	.	.	.	.	.	1	2	2	.	.	1	3	.
Crested tit	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Long-tailed tit	.	.	.	.	.	.	6	.	.	.	.	.	.	6	.	.	.	.	.	.	10	8	.	.	.	.
Whitethroat	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lesser whitethroat	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Garden warbler	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Blackcap	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Willow warbler	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Wood warbler	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Chiffchaff	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Mistle thrush	.	3	1	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Song thrush	.	2	3	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.
Redwing	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Fieldfare	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Blackbird	.	7	4	6	.	.	.	.	.	1	.	.	.	.	.	.	9	.	1	5	.	.	1	.	2	.
Redstart	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Robin	.	.	.	1	.	1	.	.	.	1	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.
Nightingale	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Dunnock	.	.	.	2	.	.	.	.	.	.	.	.	.	.	.	.	4	.	.	.	.	.	2	.	.	.
Wren	2	4	2	1	.	.	.	7	.	.	.	.	.	.	.	.	1	3	1	1	.	.	1	1	.	.
Spotted flycatcher	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Great spotted woodpecker	.	.	.	.	.	.	3	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	1	.
Lesser spotted woodpecker	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Green woodpecker	1	.	.	.	.	.	2	.	2	.	.	.	1	.	.	.	.	1	1	.	.	.	.	.	.	.
Wryneck	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Cuckoo	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Barn owl	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Tawny owl	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Little owl	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Buzzard	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.
Sparrow hawk	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Kestrel	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Heron	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Woodcock	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Stock dove	.	1	120	2	.	.	.	.	.	.	1	.	32	.	50	86	.	4	.	.	.	.	1	.	.	.
Ring dove	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	1	1	.	.	.	4	.
Turtle dove	.	.	.	.	.	.	1	9	.	.	.	.	.	.	3	4	.	.	.	.	.	.	.	.	.	.
Pheasant	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Capercaillie	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Black grouse	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

APPENDIX

COMPLETE TABULATED COUNTS FROM SURVEYS

(1) *District.* The following abbreviations are used:

S.E. South-east England (Kent, Sussex, Surrey, Hampshire).
S.W. South-west England (Dorset, Devon).
C. Home Counties (Middlesex, Hertfordshire, Oxfordshire, Berkshire, Buckinghamshire).
E. Eastern England (Cambridgeshire, Suffolk, Norfolk).
M. Midlands (Nottinghamshire, Cheshire, Shropshire, Worcestershire).
N. Northern England (Yorkshire, Lancashire, Cumberland, Westmoreland).
Sc. Scotland excluding Highlands (Midlothian, Perthshire, Dumbartonshire).
H. Highlands of Scotland (Inverness-shire).

(2) *Secondary growth.*

\+ indicates present in fair quantity.
½ indicates present but very sparse.
— absent, or almost entirely absent.

(3) *Number of counts.* Where more than one count was taken, the figures indicate the largest number of individuals of the species seen on any one walk.

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A NOTE ON THE FOOD OF PIKE (*ESOX LUCIUS*) IN WINDERMERE

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This paper is based on the examination of the stomach contents of 103 pike captured in Windermere between August 1933 and October 1935. The majority of the fish caught were taken in a seine net worked on the shores of the lake, but a few were obtained by angling. The results of the examination of a few pike netted in Rydal Water are also included in this paper, since conditions in this lake are similar in many respects to those in Windermere.

The food of pike consists principally of small fish, and this has been found to be the case in Windermere. A few of the pike had also been feeding to some extent upon invertebrate animals. Four species of fish were found in the stomachs: perch (*Perca fluviatilis*), trout (*Salmo trutta*), minnow (*Phoxinus phoxinus*), and three-spined stickleback (*Gasterosteus aculeatus*). These include all the fish common in the lake except the char (*Salvelinus willughbii*), eel (*Anguilla vulgaris*), and the pike itself. The char lives during the greater part of the year in the open water away from the shore, and only comes into shallow water when spawning. Since the pike appears to be largely confined to the littoral region of the lake, the char is therefore hardly available to it as food. But as all the pike referred to in this paper were caught near the shore, no evidence is available as to whether the few pike living in deep water feed on the char. The burrowing and bottom-living habits of the eel make it somewhat inconspicuous and therefore less available to the pike. The absence of small pike from the food of the larger ones is rather striking.

The net used for catching pike had a mesh of 2·5 cm. knot to knot, and therefore allowed pike under about 30 cm. in length to escape. The large baits used when angling for pike rarely attract fish under about this size. Consequently the sample of pike collected consisted almost entirely of fish over 30 cm. (see Table 1, which shows the size distribution of the pike caught). It is probable that this table gives a fairly accurate representation of the size distribution among the larger pike in the lake.

A comparison has been made between the stomach contents and the size of the pike, but there is no suggestion of any change in the species eaten as the pike grow larger. This, of course, does not suggest that there is no change of this nature in pike less than 30 cm. in length; and in fact it is obvious that

at one stage at least in the growth of the pike there must be a change in the type of food eaten. Balfour-Browne (1907) found that in Sutton Broad the first food of young pike fry was Entomostraca, including fairly large Daphnids.

Table 2 shows the number of pike containing each of the principal types of food. The perch is clearly the most important food. When it is considered that probably a great proportion of the fish which were too far digested to be identified were also perch, the predominance of the perch over all other foods

Table 1. *Size distribution of pike caught*

Length ... in cm.	15·0–19·9	20·0–24·9	25·0–29·9	30·0–34·9	35·0–39·9	40·0–44·9	45·0–49·9	50·0–54·9	55·0–59·9
No. of fish	1	—	2	13	15	20	12	10	11
Percentage of catch	1	—	2	12	14	19	12	10	11

Length ... in cm.	60·0–64·9	65·0–69·9	70·0–74·9	75·0–79·9	80·0–84·9	85·0–89·9	90·0–94·4	95·0–99·9	Total
No. of fish	9	6	1	—	1	1	—	1	103
Percentage of catch	9	6	1	—	1	1	—	1	100

Table 2. *The number of pike found to contain each food animal*

Food	No. of fish
Ephemera danica nymphs	6
Leptocerus larvae	1
Earthworms	1
Total with invertebrates	7
Phoxinus phoxinus	9
Gasterosteus aculeatus	8
Perca fluviatalis	42
Salmo trutta	2
Unidentifiable fish	18
Total with fish	68
Empty	32

becomes even greater. The relative numbers of perch and trout eaten by the pike correspond very approximately to their actual numbers in the lake, and it might appear that the pike showed no well-marked preference for either species. In winter, however, the perch are all in water about 20 m. deep and are practically absent from the littoral region. This is shown by the fact that during the months November to March seine netting yielded 288 trout and only two perch. Despite this the pike captured during these months contained four perch and only one trout. Thus it appears that the perch is either very much more easily caught than the trout, or else is definitely selected by the pike.

The two species of small fish eaten by the pike, the minnow and the three-spined stickleback, were eaten in approximately equal numbers. The minnow is, however, very much more abundant than the stickleback in the lake, and occurs in very large shoals. Since it has also been shown that perch which were feeding on fish contained minnows only slightly more frequently than sticklebacks (Allen, 1935), it appears likely that owing to some difference in

habit or habitat the stickleback may be rather more available to carnivorous fish than is the minnow.

Table 2 shows that the only invertebrate animal frequently eaten by the pike is the nymph of a mayfly, *Ephemera danica*. All the pike which had been eating these were caught in June, and had been taking mature nymphs, apparently as they rose to the surface preparatory to hatching.

It is clear that it is to the advantage of a fish to change its diet as it increases in size so as to increase correspondingly the size of the food particles. This frequently leads to changes in the actual type of food taken, as has been shown to occur in the perch (Allen, 1935). Pike in the size range considered in this paper do not show a change of this nature. It is also possible that among fish feeding on the same type of food the larger individuals may choose larger individual food organisms. In nearly every case where a fish was found in the stomach of a pike its length was recorded, and consequently it is possible to determine the average size of fish eaten by pike of various sizes. It was found that pike more than 38 cm. long tended to eat larger fish than did pike of less than 38 cm. The respective mean lengths of the fish eaten by these two classes of pike were 8·65 and 6·02 cm. Application of the *t*-test (Fisher, 1936) to these results shows that the probability of such a difference in the mean with random sampling was less than 0·01, so that this difference is evidently significant. No further differences of this type could, however, be found by subdividing these two classes of pike.

Table 2 also shows that the proportion of empty stomachs among the pike examined was very large. This high proportion of empty stomachs appears to be characteristic of fish-eating fish. Nilsson (1921) found that out of 38 pike stomachs examined 20 were empty. The significance of this phenomenon has been discussed in a previous paper (Allen, 1935), where it was shown that in the perch the change to a fish diet was accompanied by an increase in the percentage of empty stomachs. As in the perch, a greater proportion of empty stomachs is found in the pike in winter than in summer. Out of 32 pike caught in the months November to March, 14 (44 %) contained no food, while during April to October only 19 out of 71 (27 %) were empty. This increase in the proportion of empty stomachs in winter is very probably due to the reduced rate of metabolism in the fish at the lower temperature.

Summary

1. This paper gives the results of the examination of the stomach contents of 103 pike, taken chiefly from Windermere.

2. The fish examined, few of which were less than 30 cm. long, had been feeding almost entirely upon other fish, principally perch.

3. The only invertebrate food taken to any great extent was hatching nymphs of *Ephemera danica*.

4. Pike less than 38 cm. long tended to eat rather smaller fish than did larger pike.

5. The percentage of pike with empty stomachs was high at all times, but higher in winter than in summer.

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A SURVEY OF THE STATUS OF *RATTUS RATTUS* AND ITS SUBSPECIES IN THE SEAPORTS OF GREAT BRITAIN AND IRELAND

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(*With 5 Figures in the Text*)

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1. Introduction

The history of *Rattus rattus* and of *R. norvegicus* in this country is familiar to most zoologists, and only a few words need be said on the subject here. The black rat (*R. rattus*) is believed to be an alien which first reached our shores some time in the Middle Ages, a common suggestion being that it was brought back from the east on the ships of the Crusaders; at any rate it was an established and numerous member of our fauna for several hundred years, and the only species of rat existing in Britain. The brown rat (*R. norvegicus*) is an alien which is known to have appeared for the first time in Britain about the beginning of the eighteenth century. (Regarding the reported occurrence of bones of *R. norvegicus* in deposits at Kilgreany Cave, Ireland (**5**), Dr Wilfrid Jackson has written to me: "The upper levels were loose and somewhat disturbed, and I think the brown rat is a fairly recent intrusion there.") This is a larger animal than the black rat and more adaptable generally, and there seems little doubt that it was responsible for the complete disappearance of the latter from most parts of the British Isles.

In many districts the black rat had been driven out before the end of the eighteenth century, though it survived, in dwindling numbers, in some inland places till about the middle of the nineteenth or later (**6**). During the latter

part of the nineteenth century it seems to have disappeared entirely, except in a few islands and some of the seaports on the mainland. Whether it ever became quite so scarce at these ports as is often stated, may be doubted. The following extract from an article in *Notes and Queries* of 1854 (10: 335) is suggestive: "In 1845...there was an intelligent man, and not a bad naturalist for his station in life, who exhibited a "Happy Family" opposite the National Gallery. He generally had three or four black rats in his cage....He informed me that he had long known that the black rat inhabited the upper parts of the old houses in St Giles's; and that when applied to by naturalists for a specimen of the animal, he took care to represent its exceeding rarity, though by setting traps in these houses he could catch one almost whenever he pleased. He also stated that his usual price for a specimen used to be three guineas." At Great Yarmouth there was a colony which was the subject of a series of notes from 1896 onwards (**7**, **8**).

In later years, the species was found to exist in some numbers at various ports, and the usual assumption appears to have been that these numbers were kept up by specimens escaping from ships. For example, with regard to the Yarmouth colony, Patterson, as quoted by Hinton (**4**), wrote in April 1918, that they were now "becoming rarer....The war allows no grain ships here, so that the species does not now breed ahead of its destruction." *R. rattus* is, it may be noted, by far the commoner species on ocean-going vessels, the brown rat being usually entirely absent. Thus, of the total number of rats destroyed on ships in Cardiff Docks by the rat-catcher during the years 1922–8 inclusive, 22,036 were black rats and only 50 were brown; at Liverpool, from 1929 to 1937 inclusive, 28,956 ship rats were of the black species, and only 72 were brown.

In recent years there has been a great intensification of efforts to eradicate rats on board ships. One object of the present enquiry was to illustrate the work done in this respect at British seaports and its results; but the main object was to determine, if possible, whether the decrease of black rats on ships visiting British ports had resulted in any corresponding decrease of black rats on shore—in other words, whether the black rat population on shore is dependent on immigrants from ships or can be regarded as an established part of our mammalian fauna. It will be advisable at this point briefly to outline the measures against rats adopted at all the bigger ports at the present time.

Formerly, rat-infested vessels arriving in British ports were dealt with under the powers conferred by the Rats and Mice (Destruction) Act, 1919. At Cardiff, for example, in 1926, 42 notices were served on masters of vessels under the Act; 23 vessels were fumigated (resulting in the death of 575 rats and 18 mice), and the rat-catcher carried on operations on board 55 vessels. Enquiries were made on board every vessel arriving at the port as to the presence of rats. The vessels reported to be rat-infested on arrival were examined by inspectors,

while many vessels were found on inspection to be infested, although reported rat-free on arrival.

The procedure has now been greatly modified as a result of Article 28 of the International Sanitary Convention of Paris, 1926, which recommended that the master of every vessel coming from a foreign port should have to produce a certificate issued within the last six months, at an approved port, stating either that the vessel had been deratized there (deratization certificate), or had been found on inspection to be free from rats (exemption certificate). This recommendation was widely adopted from 1928 onwards; thus at Cardiff in 1929, 181 deratization and 110 exemption certificates were issued to masters of ships. Article 28 of the Paris Convention was subsequently made compulsory by the Public Health (Deratization of Ships) Regulations, 1929, which came into effect on 1 January 1930 and are now incorporated in the Port Sanitary Regulations, 1933.

In addition to measures designed to reduce the number of rats on ships, British ports to-day adopt many precautions to prevent the passage of rats from ship to shore, or vice versa. The following summary of the methods in operation at Southampton will serve as an illustration, these methods being in essentials the same at all ports. (1) The ship must be so moored as to be at no point less than 6 ft. from the quay. (2) All warps, etc., used for mooring must be fitted with canvas rat-guards (coated daily with tar) or with shields or disks. (3) No gangways or planks connecting ship and shore are allowed except that in actual use; and the latter, if not in constant use, must have a man in attendance day and night and be provided with a light at night. (4) Booms and other appliances keeping the ship in position and connecting it with the quay must be coated with tar parcelling and the tar renewed daily.

It is, however, probable that a number of rats still get ashore: one Medical Officer of Health, in his *Annual Report*, suggests that the majority do not land "via the mooring ropes, etc., but are landed with cargo in crates, etc...." The chief object of the present enquiry was to ascertain whether the intensive methods of rat destruction on ships now in force at British ports have in fact resulted in any definite decline of the black rat population on shore. As will be clear from the preceding paragraphs, the new regulations regarding rat destruction on vessels have now been obligatory at all ports for over nine years, and were actually adopted at many ports still earlier; so sufficient data should be available to furnish a definite indication of the effects on *R. rattus* both on ships and ashore.

2. Questionnaire

With the collaboration of Dr J. Greenwood Wilson, Medical Officer of Health for the City and Port of Cardiff, a questionnaire was drafted asking for information on the following points:

(1) The numbers of black rats and of brown rats destroyed (*a*) on ships,

(*b*) on docks, quays, wharves, and in warehouses and other premises ashore, in each year from 1925 to 1937 inclusive.[1]

(2) In the case of black rats, the numbers (if available) destroyed of each subspecies—*R. rattus rattus*, *R. r. alexandrinus* and *R. r. frugivorus*.

(3) Any known factors, apart from an actual decrease or increase in the rat population, which might affect the total number of rats destroyed from year to year, e.g. whether the amount of rat-catching conducted has fluctuated or remained fairly constant over the period 1925–37.

(4) Number of ships examined for rats each year, number of ships fumigated, and number of rats found dead per ship after fumigation, during the period 1925–37.

(5) Any information available as to the ratio of male to female rats.

(6) In general, any observations of interest you may care to make on the rat situation in your port health district.

A copy of this questionnaire was sent, with a covering letter, to the Medical Officer of Health of the Port Health Area of each "approved port" in Great Britain and Ireland. With the exception of the data for Cardiff, which are largely the result of the writer's own records, the present paper is based mainly on 22 replies received to this questionnaire; though some of the replies cover too short a period, or are not sufficiently detailed, for use in the tables and graphs. To the Port Medical Officers concerned, and in particular to Dr J. Greenwood Wilson, I wish to tender my grateful thanks.

3. England and Wales

(*a*) *Black rats on ships: results of fumigation*

There can be little doubt that rat infestation of ships is now very much less than formerly. Fumigation of a ship in London Docks is recorded to have yielded as many as 1700 dead rats (**3**). The difference to-day is well illustrated by the following quotation (relating to all the ports in England and Wales) from the *Annual Report* for 1936 of the Chief Medical Officer of Health. "The largest number of rats recorded from any one ship as a result of fumigation was 338. . .it is now rare to find anything approaching this degree of infestation." At the Port of London, the average number of rats per ship found dead after fumigation has in recent years varied from about four to six. The replies sent to query 4 of the questionnaire include records of four ships at one port in 1927,

[1] The classification into black and brown is of course done by the lay staff, but the probability of any important error is small. The inspectors, etc. concerned are trained to distinguish the species; and as the great majority of ship rats are correctly recorded as black (despite the resemblance of the common subspecies *alexandrinus* to the brown) the records on shore may be taken as equally correct. Any error that did occasionally occur would lie in recording black rats (*alexandrinus* type) as brown—no brown rat (save infrequent melanic specimens) could ever be recorded as black; and such an error if corrected would obviously strengthen, instead of weakening, the conclusions drawn in this paper.

with an average of 235·5 rats per ship, and one ship at another port in 1933 with 100 rats; but at these and other ports such figures are now very uncommon.

Seven ports have supplied statistics going back to 1925, and the average number of rats found per ship after fumigation, calculated on the aggregate figures for these seven ports, was as follows for the earlier years, before the general adoption of the recommendations of the Paris Convention: 1925, 30·4 rats per ship; 1926, 23·0; 1927, 23·0; and 1928, 20·6 rats. Fig. 1, based

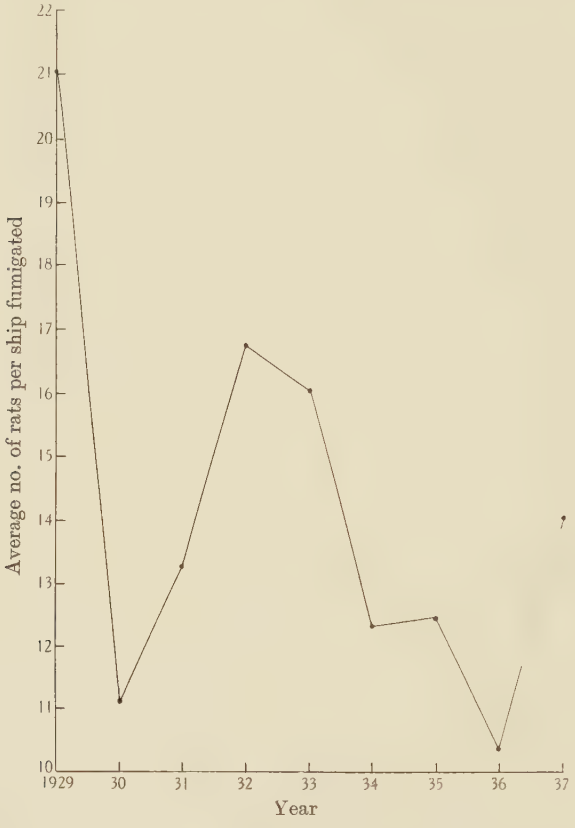

Fig. 1. Average number of rats per ship found dead after fumigation in each year from 1929 to 1937. (Based on the figures for ten seaports in England and Wales—see Table 1.)

on the statistics for ten seaports in England and Wales (Table 1), indicates the average number of rats per ship found dead after fumigation, in each year from 1929 to date. It appears that, since 1929, the average number of rats has not greatly altered, fluctuating around a figure of about 13 rats per ship. This general conclusion holds for most of the ports individually, as study of Table 1 will show; the actual figure for rats per ship varies, of course, from port to port, but the figure at each port has of late shown little decrease from year to year. (This applies also to the statistics for Hull, received too late for inclusion in the

Table 1. *Number of ships fumigated, and average number of rats per ship found dead after fumigation, at ten seaports in England and Wales, for each year from* 1929 *to* 1937

	R. Blyth		Bristol		Cardiff		Liverpool		Manchester		Middlesbrough		Newport		Southampton		Sunderland		Swansea		Totals, and av. no. rats per ship, for all ports		
Year	Ships fumigated	Rats per ship	Ships fumigated	Rats per ship	Ships fumigated	Rats per ship	Ships fumigated	Rats per ship	Ships fumigated	Rats per ship	Ships fumigated	Rats per ship	Ships fumigated	Rats per ship	Ships fumigated	Rats per ship	Ships fumigated	Rats per ship	Ships fumigated	Rats per ship	Total ships fumigated	Total rats found dead	Av. no. rats per ship
1929	1	50	28	8·0	181	37·0	221	7·80	19	8·74	13	25·9	97	19·8	23	8·20	14	86·3	20	23	617	12,976	21·03
1930	3	22	49	12·2	236	18·0	187	3·50	15	20·0	23	8·9	83	7·0	17	7·6	21	12·2	26	11	660	7,324	11·10
1931	13	10	27	16·6	195	18·1	162	2·02	19	8·0	13	26·8	59	15·0	12	7·5	52	20·0	30	26	582	7,730	13·28
1932	6	51	23	26·2	121	30·8	142	2·03	23	11·2	10	10·1	28	12·1	15	1·6	47	28·9	28	10	443	7,415	16·74
1933	10	12	26	33·2	124	28·5	137	2·05	18	16·2	22	13·9	43	16·8	11	1·09	40	18·7	40	17	471	7,557	16·04
1934	10	12	29	25·5	126	20·5	154	2·06	19	21·0	26	15·3	43	15·5	11	0·09	33	15·7	36	7	487	5,995	12·31
1935	17	18	19	32·8	109	17·5	172	2·09	13	14·0	24	27·5	49	15·2	15	0·86	9	52·3	34	14	461	5,744	12·46
1936	7	6	19	16·1	126	12·0	153	1·75	15	41·5	21	15·8	41	17·6	19	0·68	12	18·5	26	20	439	4,559	10·38
1937	5	7	16	18·3	121	11·0	153	2·29	12	58·4	28	21·5	57	40·6	15	1·3	15	25·0	25	10	447	6,271	14·03

Table 2. *Average number of rats destroyed per ship subjected to measures of rat destruction in all the approved seaports of England and Wales for each year from* 1926 *to* 1936 *inclusive*

(Calculated from the statistics in the Annual Reports of the Chief Medical Officer of the Ministry of Health)

Year	No. of ports concerned	No. of vessels subjected to measures of rat destruction	No. of rats destroyed on ships	Average no. of rats destroyed per ship subjected to rat-destruction
1926	13	3072	52,944	17·23
1927	12	3567	42,473	11·91
1928	12	3420	43,987	12·86
1929	17	4737	52,508	11·08
1930	21	5433	33,978	6·25
1931	21	4429	33,070	7·47
1932	22	5194	32,859	6·33
1933	22	3549	30,503	8·59
1934	23	3351	27,815	8·30
1935	23	3034	23,419	7·72
1936	23	3110	24,876	8·00

tables.) Additional confirmation is supplied by Fig. 2 and Table 2, which show the average number of rats destroyed per ship subjected to measures of rat destruction (trapping, poisoning etc., as well as fumigation) in all the approved seaports of England and Wales, for each year from 1926 to 1936; there has been no decrease in the average number of rats per ship in the period since 1929.

Somewhat different is Fig. 3, which is based on the aggregate statistics

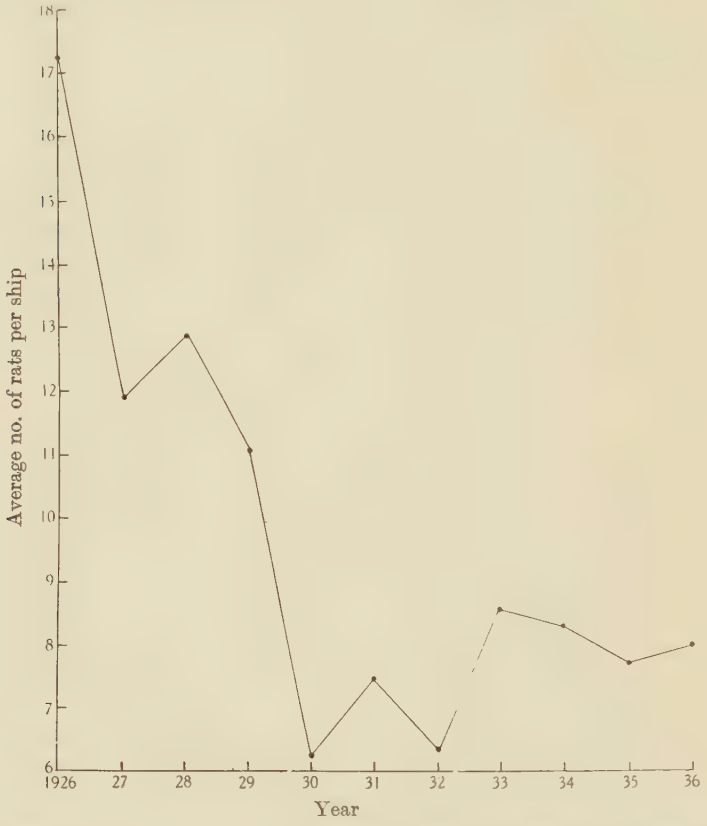

Fig. 2. Average number of rats destroyed per ship subjected to measures of rat-destruction in all the approved seaports of England and Wales, for each year from 1926 to 1936 inclusive.

(Table 3) for the same ports as Fig. 1 (with one omission, for which particulars were not available). This figure shows the number of ships fumigated each year, from 1929 onwards, as a percentage of the total number examined each year for rats. The curve is practically free from fluctuations and shows that, of the vessels examined, the proportion found to require measures of rat destruction is steadily, though now very slowly, decreasing year by year. This conclusion, as Table 3 will show, applies also to most of the ports individually.

Studied in conjunction, then, Figs. 1, 2 and 3, and the corresponding tables,

Table 3. *Number of ships examined for rats, and number of ships fumigated, at nine seaports in England and Wales, in each year from 1929 to 1937*

Year	Bristol		Cardiff		Liverpool		Manchester		Middlesbrough		Newport		Southampton		Sunderland		Swansea				
	No. ships examined	No. ships fumigated	No. ships examined	No. ships fumigated	No. ships examined	No. ships fumigated	No. ships examined	No. ships fumigated	No. ships examined	No. ships fumigated	No. ships examined	No. ships fumigated	No. ships examined	No. ships fumigated	No. ships examined	No. ships fumigated	No. ships examined	No. ships fumigated	Total ships examined	Total ships fumigated	% fumigated
1929	2478	28	291	181	335	221	1232	19	93	13	130	97	163	23	482	14	683	20	5887	616	10·46
1930	3378	49	656	236	503	187	1332	15	182	23	145	83	201	17	845	21	578	26	7820	657	8·40
1931	2936	27	602	195	476	162	1359	19	156	13	141	59	212	12	908	52	730	30	7520	569	7·57
1932	2424	23	532	121	489	142	1396	23	161	10	127	28	222	15	880	47	716	28	6947	437	6·29
1933	2127	26	477	124	553	137	1404	18	133	22	126	43	237	11	804	40	793	40	6654	461	6·93
1934	2346	29	454	126	573	154	1514	19	146	26	125	43	283	11	737	33	754	36	6932	477	6·88
1935	2197	19	466	109	562	172	1566	13	169	24	132	49	266	15	814	9	873	34	7045	444	6·30
1936	2284	19	421	126	574	153	1580	15	213	21	101	41	259	19	818	12	819	26	7069	432	6·11
1937	2313	16	409	121	649	153	1654	12	226	28	143	57	230	15	933	15	836	25	7393	442	5·98

Note. Of the ships examined, the percentage requiring fumigation is very gradually decreasing. Table 2 illustrates the same tendency in a different way—the number of "approved" ports rose from 17 in 1929 to 23 in 1936, yet the total number of vessels requiring rat-destruction measures fell from 4737 in the former to 3110 in the latter year.

suggest that the average number of rats per rat-infested ship has of late years been reduced to about the smallest figure practicable at each port under existing conditions; and that an increasing number of ships is found to be free of rat infestation. The latter suggestion is also borne out by the increasing proportion of exemption (as compared with deratization) certificates issued at many British ports to masters of vessels arriving from abroad.

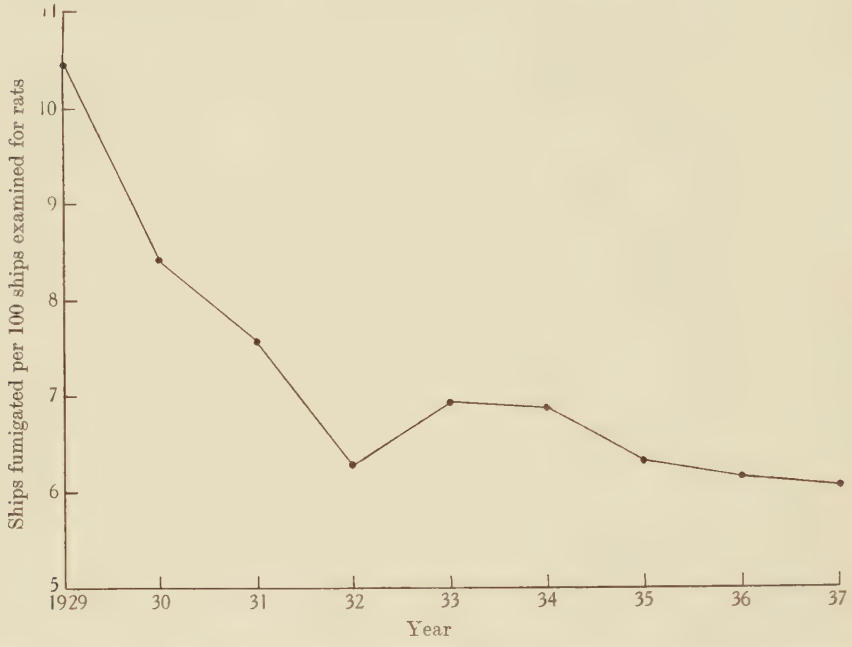

Fig. 3. Number of ships fumigated as a percentage of ships examined for rats, in each year from 1929 to 1937. (Based on the figures for 9 seaports in England and Wales—see Table 3.)

(*b*) *Black rats on shore*

Turning now to the black rats caught on shore in the various Port Health Areas each year, on docks, quays, and in warehouses, etc., it will be seen from Fig. 4 and Table 4 that in the aggregate the numbers show a definite upward tendency. (The part of the curve from and including 1929 onwards is based on the returns for thirteen English and Welsh ports; prior to 1929 the number of ports making returns of black rats caught was smaller.)

Regarding the individual ports, it would appear that with few exceptions, according to the replies received to the questionnaire, no extraneous factors (such as any great variation in the amount of rat-catching), which might significantly affect the figures between 1925 and 1937, are known (see last column, Table 4); so that a definite increase or decrease in the figures should indicate an actual upward or downward tendency of the black rat population in the port concerned. We find, then, that in three of the ports—Grimsby,

Table 4. *Total number of black rats recorded from docks, quays, wharves and in warehouses and other premises ashore at various seaports in England and Wales, in each year from* 1925 *to* 1937

Port	1925	1926	1927	1928	1929	1930	1931	1932	1933	1934	1935	1936	1937	Any known factors affecting figures, e.g. whether rat-catching fluctuated or remained constant
R. Blyth	0	0	0	31	16	34	0	3	0	7	0	0	0	—
Bristol	-	-	-	—	1001	1152	1522	1368	1099	1655	849	592	592	"Fairly constant since 1928"
Cardiff	349	207	343	385	225	454	165	102	—	65	114	92	49	Has remained constant
Dover	0	0	0	0	0	2	0	0	0	0	0	0	0	No information
Grimsby	—	—	940	720	654	786	1170	757	401	1292	988	1137	1224	"Fairly constant"
Liverpool	1699	2165	1651	1947	1324	1637	1405	1968	1849	2479	3074	2870	2454	"Fairly constant over the period mentioned"
Middlesbrough	—	—	0	100		6	4	9	54	350	311	216	456	"No known factor"
Newport	24	3	7	1	0	0	0	0	0	0	0	0	0	"Has fluctuated"
Plymouth	—	—	34	97	125	200	205	270	165	96	114	35	21	"Has fluctuated very little"
Southampton	384	397	242	147	290	603	54	11	5	0	0	28	2	"Has remained constant until 1936"
Sunderland	—	26	12	97	92	62	0	24	58	19	16	8	12	"Trapping and poisoning constantly"
Swansea	599	140	236	43	31	74	124	110	175	407	543	543	523	"Fluctuated previous to 1934"
Weymouth	32	41	66	73	352	83	199	189	140	67	20	41	29	"Has remained fairly constant"
Totals	3087	2979	3531	3641	4110	5093	4848	4811	3946	6437	6029	5562	5362	

Liverpool and Middlesbrough—the numbers of black rats taken yearly on shore have increased during the period under review, while in one (Swansea)—having regard to fluctuations in rat-catching previous to 1934, and comparing 1925 and 1937—the numbers seem at any rate not to have decreased.

On the other hand (omitting Dover and one or two others where the data seem rather few to be significant), there are six or seven ports where the figures

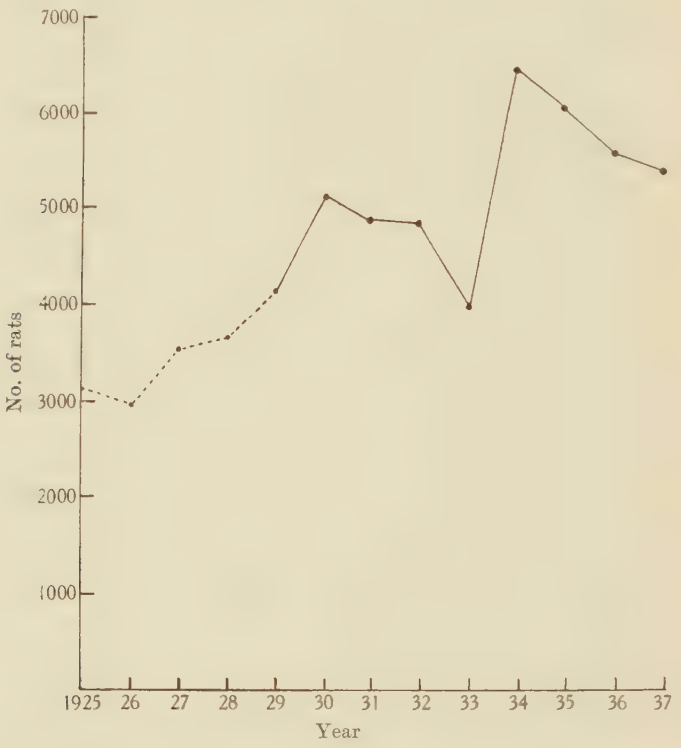

Fig. 4. Total number of black rats recorded from shore premises at the docks each year in a number of British sea-ports. (Since and including 1929 the number of ports is 13; previously it was smaller—see Table 4.)

show more or less clearly a downward trend. This is obvious for example at Cardiff and Southampton over the whole period 1925–37. There are, however, certain facts which must be borne in mind in the case of ports where black rats have decreased at the docks.

(1) In at least one of these ports (Cardiff) there appears to be an established if not increasing population of black rats in the City Area. In each year since and including 1928, the writer has examined a large number of rats from the City of Cardiff (as distinct from those examined from the Port Health Area). In the earlier years of the investigation, the great majority of all rats, whether brown or black, taken by the city rat-catcher were examined in order to collect

their fleas; but latterly, the examination of brown rats has ceased, because sufficient data on their fleas had been obtained, so that since 1934 the only rats examined from the City Area have been black ones. Comparison of the figures for the Port Health Area and for the City indicates that while the black rat has decreased in the former, it has somewhat increased in numbers and range in the latter. The details are as follows:

Year	Average no. of rats (*R. rattus*) found dead per ship after fumigation	No. of *R. rattus* identified from docks, quays, wharves, etc., in Port Health Area*	No. of *R. rattus* examined from the City Area
1928	41·8	385	37
1929	37·0	225	38
1930	18·0	454	48
1931	18·1	165	157
1932	30·8	102	71
1933	28·5	—	201
1934	20·5	65	37 (5 months only)
1935	17·5	114	86 (figures incomplete)
1936	12·0	92	121
1937	11·0	49	129
1938	11·0	64	274

* These figures represent only the specimens definitely identified as *R. rattus*. Considerable numbers of rats found dead as the result of baiting are not recorded as to species, but the downward trend of the total figures from year to year is found on comparison to be quite adequately represented by the above series.

The increase in the numbers of *R. rattus* caught in the city cannot be put down to any intensive development of rat-catching, which has been prosecuted with equal vigour throughout.

Fig. 5 shows that the range of *R. rattus* within the City Area also appears to have increased to some extent. The species has been obtained from various types of premises—private houses, shops, hotels and cafés, cinemas (including one of the most modern in the city, built in 1921), works, a tramway depot, etc.; and in all stages of development. While there is a good deal of evidence for the usual idea that the black rat frequents the upper stories of premises while the brown prefers such places as cellars, this distribution depends, of course, on local conditions. In this connexion reference may be made to Benick's list of the numbers found in each of several types of habitat at Lübeck (**1**). The Cardiff city rat-catcher informs me of one case where brown rats were found in the hollow space under the stage in a cinema, while black ones were living below in the basement—in order, he thinks, to be near the heating apparatus.

Whether the efforts to exterminate the black rat on ships and shore-premises adjoining the docks have driven the species farther afield is a suggestion worth consideration. At any rate, the facts indicate fairly clearly that the reduction of the black rats around the docks has not been accompanied by any reduction of the black rat population in the City Area. This appears to be true even in greater measure of the City of London; I have no actual statistics, but Mr E. C. Read, Chief Rat Officer to the Ministry of Agriculture and Fisheries,

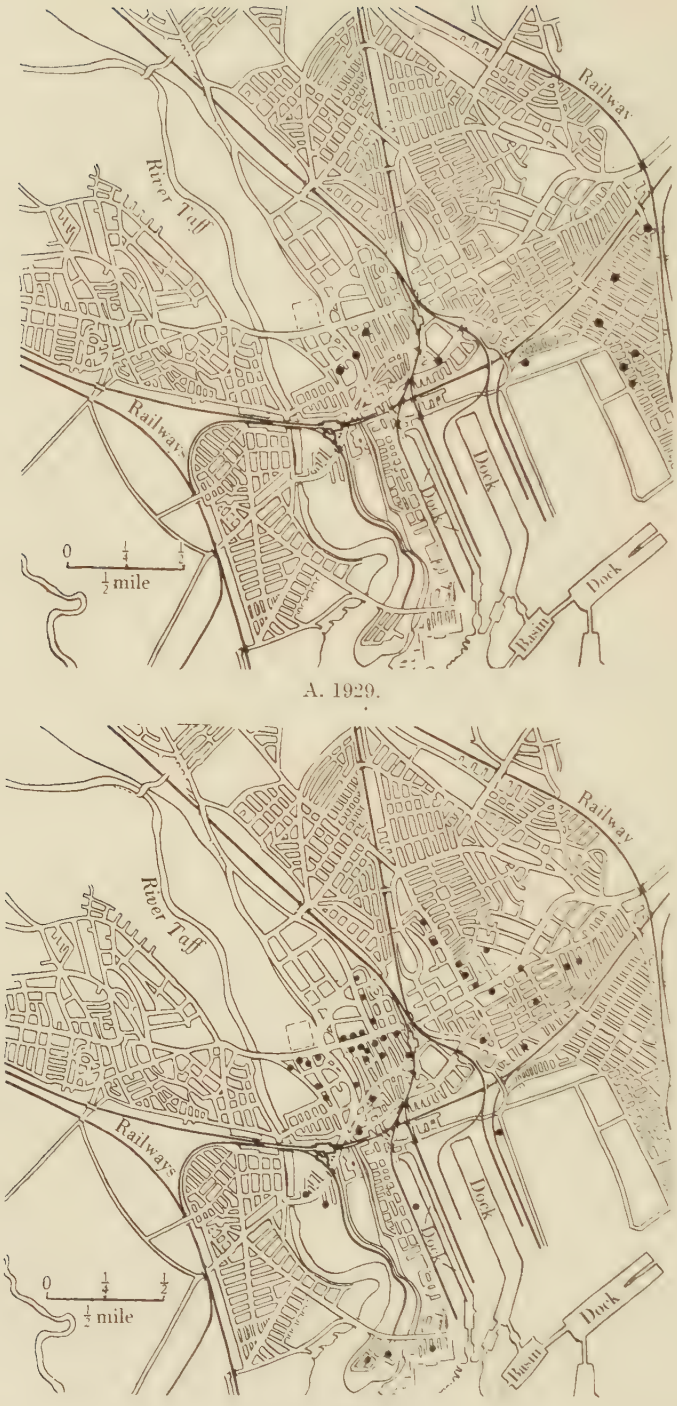

Fig. 5. Plan of the city of Cardiff, showing localities from which black rats were received in 1929 (A) and 1938 (B). (*Note*: In both plans only black rats from the City Area, not from the docks, are recorded.)

states in a letter of 3 March 1938: "To my own personal knowledge the rat population of the City of London is approximately 90% *Rattus rattus* with a great preponderance of *alexandrinus*." This, despite the fact that at the Port of London, the average number of rats per ship found dead after fumigation decreased from 12·71 in 1926 to 4·21 in 1936.

There may be other ports in which the black rat is established at a distance from the docks. Liverpool, for example, has a black rat population in the City Area, though this is relatively small and appears to be decreasing: in 1930, of 16,899 rats caught in the City, 2060 were black; in 1931, of 15,755 rats, 1580 were black; in 1934, of 16,687 rats, 1129 were black; while in 1936, out of a total of 14,331, only 456 were of the black species. On the other hand, Liverpool is one of the ports which, as shown in Table 4, still has an undiminished black rat population at the docks.

It is suggested by Hinton (**4**) that the efforts of the black rat to recolonize our cities have been greatly aided in modern times by "rebuilding and the rat-proofing of basements (which has shut out *R. norvegicus*), and by the extension of the telephone system and the removal of kitchens from basements to roofs". And a striking illustration of the position in a large modern American city is afforded by the fact that, of the total number of rats taken by the trappers in San Francisco during the years 1936 and 1937, almost one quarter were *R. rattus*, "found almost exclusively in the section of the city that was rebuilt after the great fire of 1906" (**2**).

There are then several ports in England and Wales which, despite nine to ten years of very efficient ship-deratization work, still have an undiminished if not increasing population of black rats on shore, either around the docks or in the city.

(2) The question also arises whether, in those ports where black rats have decreased on shore premises in the Port Health Area, there has been a *general* decrease of the rat population, both black and brown. If so, then since the brown rat population is essentially a land one, being for example entirely negligible on board ships at ports like Cardiff, Plymouth and River Blyth, it seems clear that the decrease of brown rats on shore does not have much connexion with the decreasing rat-infestation of shipping; and the inference (known to be correct in some cases) is that the decrease of both species around the docks in such ports is due to causes (e.g. improved reconstruction of warehouses, etc.) other than ship-deratization measures. In these ports, then, where the black rat population on shore at the docks has decreased, the suggestion that this population is mainly derived from ships and has declined as a result of modern ship-deratization, though possibly valid in some cases, receives actual support from the statistics only where the decrease in the black rats is not accompanied by any decrease in the brown; the only cases of this kind, among the ports supplying information, being Bristol and Sunderland.

4. Scotland and Ireland

Black rats on ships and ashore

The Scottish ports from which replies were received to the questionnaire were Edinburgh, Glasgow, Dundee, Ayr, Grangemouth and Greenock. Glasgow is, however, the only one to supply data that are readily comparable throughout with those for the English and Welsh ports, particularly on the main point at issue—the status of *R. rattus* ashore. The data may be tabulated as follows:

Year	No. of ships examined for rats	No. of ships fumigated	Average no. of dead rats per ship after fumigation	No. of black rats destroyed on docks, quays, wharves and in warehouses, etc.
1929	1651	127	17	97
1930	1625	127	17	371
1931	1451	173	12	97
1932	1394	119	13	46
1933	1404	112	18	150
1934	1513	126	17	306
1935	1510	107	26	503
1936	1564	130	27	732
1937	1624	133	19	618

Regarding the figures for ship fumigation, Dr A. S. Macgregor, the Medical Officer of Health, observes: "In the table given above there is an increase in the number of rats per ship during the past three years and this, it is stated, may be due to more foreign ships being dealt with, especially those of Greek registration."

With reference to the position on shore, "the assistant inspector who immediately supervises the fumigation of ships states that outside the docks he has seldom or never seen black rats. The number of rats in the docks, he says, varies from time to time with the cargoes that may be brought in from ships which are either ratty or not." It will be noted that the number of black rats taken annually on shore premises, which does not appear to be decreasing, has in fact been particularly large during the last three years, these being also the years when the average number of rats per ship fumigated was highest.

At Dundee, figures are available for the black and brown rats taken on shore premises in the Port Area for the three years 1935–7; previously only the total number of rats, irrespective of species, having been recorded. In 1935, 406 brown rats were taken and only 4 black; in 1936, 164 brown and 10 black; in 1937, there were only 126 brown rats but the black had increased to 62.

The only replies received from Ireland to the questionnaire were from Dublin and Belfast. At Dublin the number of ships fumigated, and the average number of rats found dead per ship, are very small—about two ships per year, with an average of only two to three rats per ship; as the Medical Officer observes, the greater proportion of foreign ships make their first call at English ports, where rigid preventive measures are in operation, while in other ports

trading with Dublin large staffs are employed for the purpose. "There is, therefore," he says, "a very appreciable lessening of our deratization measures on these vessels." Nevertheless, on shore, from 1932 to 1937 inclusive, 71,580 rats were destroyed on docks, quays, wharves, etc., at Dublin; this large number being mainly accounted for by the fact that during the years 1933 to 1936 "the Dublin Port and Docks Board (the governing body of the entire dock system) engaged the services of a contractor to carry out rat-repression methods"; it is stated that of the total "about 80% belonged to the brown variety". *R. rattus* must still be common enough on shore if about 14,000 of them were accounted for during those six years.

With regard to Belfast, the data relevant to the present enquiry may be tabulated thus:

Year	No. of ships examined for rats	No. of ships fumigated	Average no. of dead rats per ship after fumigation	No. of black rats destroyed on docks, quays, wharves and in warehouses, etc.
1929	59	13	14	72
1930	97	23	3	91
1931	66	20	12	210
1932	68	12	7	302
1933	77	7	5	222
1934	63	9	5	213
1935	54	3	9	261
1936	75	7	6	164
1937	74	5	2	286

Here, again, the number of black rats destroyed on shore shows no sign of a decrease during the past nine years, although the amount of rat-catching conducted is stated to have been "fairly constant" over that period.

5. Relative numbers of the three subspecies of *Rattus rattus*

As is well known, the species *R. rattus* occurs on ships and on shore in Europe in three definite colour and pelage phases, which may be regarded as subspecies; *R. r. rattus*, with black back and smoky grey belly, a type characteristic of, and probably originating in, the cold temperate countries of Europe; *R. r. alexandrinus*, with brownish grey back and dingy belly, a type particularly characteristic of Asia Minor and North Africa; and *R. r. frugivorus* —in which the brighter brown of the back is separated by a sharp line from the pure white of the belly—distributed widely in the Mediterranean region.

Statistics are available from four of the ports as to the relative numbers of each subspecies found there, and although the differentiation is usually done by the lay staff, a fact which should be borne in mind when considering the figures, it is quite easy with a little practice to distinguish the three types. The writer has for years been able to assign this task to a lay member of the staff of his own department, knowing from experience that mistakes were of very rare occurrence.

Mr E. C. Read's statement that the great majority of the black rats taken in the City of London are of the subspecies *alexandrinus* has already been mentioned, and so far back as 1890, it would seem from a note in *The Zoologist* of that year (p. 135), a considerable number of the rats at Jamrach's animal establishment in East London were of the *alexandrinus* type. Of six specimens kindly sent to me by Messrs Wm. Dalton and Sons as a sample of the City of London rat population, only one was a typical *rattus*, three were typical *alexandrinus*, while two appeared to be crosses. At Plymouth *alexandrinus* is also said to be the most numerous to-day: the Deputy Medical Officer states, in reply to the questionnaire, that *R. r. alexandrinus* is the type "most commonly met with; *R. r. rattus* to some extent; *R. r. frugivorus* not noticed".

At Glasgow, Liverpool, Hull, and Cardiff the state of affairs, as shown by records extending over a period of nine years or longer, is somewhat different. At Glasgow the total numbers of each subspecies (from ships and docks), destroyed during the years 1929–37 inclusive, were as follows; *R. r. rattus*, 10,526; *R. r. alexandrinus*, 9960; *R. r. frugivorus*, 9627; each being the most numerous in three out of the nine years. The three forms therefore appear to occur with about equal frequency, the typically northern form *rattus*, the so-called "old English black rat", which was our common British rat until about two hundred years ago, being slightly the most numerous.

At Liverpool the figures for *R. r. rattus* only are given separately, those for the other two subspecies being combined. From 1930 to 1937 inclusive *rattus* numbered 18,966, while *alexandrinus* and *frugivorus* together numbered 20,962; it would appear therefore that *rattus* is definitely predominant at Liverpool. Similarly, the figures for Hull and Goole, which go back to 1925, show a total of 40,110 *rattus* and only 22,649 of the other subspecies; *rattus* being the most common in 10 out of the 13 years.

At Cardiff, the writer has kept records of the numbers of each subspecies he has examined from the Port from 1926 to 1938, and has also some data for previous years. The total numbers of each, from ships and docks, warehouses, etc. in the Port Health Area, examined in the Department of Zoology at the National Museum of Wales during this period were—*R. r. rattus*, 1711, *alexandrinus*, 434; *frugivorus*, 1029. From the City, as apart from the Port Area, the numbers examined were: *rattus*, 876; *alexandrinus*, 84; *frugivorus*, 351. It is clear that, both at the docks and within the city, *rattus* is the most numerous, *frugivorus* fairly common, while *alexandrinus*, contrary to the state of affairs described at London and Plymouth, is quite definitely the rarest instead of the commonest type. This holds not only for the aggregate figures but from year to year; in 14 out of the 17 years 1922–38, *rattus* was the most, and *alexandrinus* the least numerous among the specimens received from the Port; while during the eleven years in which rats have been examined from the City Area, *rattus* was the commonest throughout and *alexandrinus* the scarcest.

In brief, therefore, at three ports on the west coast—Glasgow, Liverpool

and Cardiff—and at Hull on the north-east coast, *rattus* is in greater or less degree the dominant subspecies, whereas in London and Plymouth *alexandrinus* is stated to occupy this position. Whether it would be possible to establish any connexion between the form of black rat chiefly found at a port, and the type and nationality of the bulk of the shipping there, is an interesting speculation, but one which is outside the scope of the present paper.

The subspecies of the black rat formerly found in London, as in other parts of Great Britain, was the "old English black rat", *R. r. rattus*; the fact that *alexandrinus* is now the most frequent there suggests that the black rat population of modern London originated in the first place from shipping, and not from any revival within the city of the old type; but however it originated, it seems now to be firmly established without requiring any augmentation from the rapidly dwindling numbers of ship rats.

6. SUMMARY

Statistics are given to show that the average number of rats (which are almost invariably black rats) per ship fumigated at British ports, and the percentage of shipping requiring fumigation, have declined considerably within the 13 years 1925–37; while many precautions are taken to prevent, as far as possible, the passage of rats between ship and shore.

Despite this, several ports still show an undiminished black rat population on shore—at the docks and, in some cases, in premises at a distance from the docks. In those ports which show a decrease in the black rat population on shore, comparison with the figures for brown rats indicates in most cases that the decrease applies to both species, and is not therefore necessarily related to ship deratization measures.

It seems clear therefore that the black rat is capable of maintaining itself in some numbers in various types of premises at British seaports, without receiving any notable additions to its numbers from ships.

From statistics quoted, it appears that *R. r. rattus* is in greater or less measure the most frequent subspecies found at three ports on the west and one on the north-east coast; whereas at London and Plymouth the commonest subspecies is stated to be *alexandrinus*.

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AN ATTEMPT TO DETERMINE THE ABSOLUTE NUMBER OF RATS ON A GIVEN AREA

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(*With* 3 *Figures in the Text*)

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1. Introduction

One of the most interesting problems for the ecologist is the estimation of the density of a particular animal species and in an attempt to determine this a system of trapping is among the devices most commonly employed. The reaction between a number of traps and a population of animals is essentially a special case of the predator-prey relationship; and perhaps it would not be too much to say that the experimental study of this trap-animal reaction is fundamental to the development of quantitative ecology in the field. The proper procedure would be to formulate a theory of trapping in the simplest terms possible and then to experiment with a given number of animals under known conditions. On the comparison of the results with the equations deduced from theory would depend whether the hypothesis be accepted or recast. The observations discussed in this paper were made in order to see whether any consistent results could be obtained by means of a standardized trapping method: they are not experiments in the sense we have outlined since the number of animals at risk was unknown. But, although a number of details will be noticed in which, from this point of view, an improvement or economy of design might have been achieved, the design as a whole fulfilled certain essential conditions of such an experiment. It is interesting to observe that the arithmetical analysis of this data has not revealed any result which

is inconsistent with the fundamental hypothesis. Logically this does not mean that its truth is to be accepted; indeed it would be surprising if such an elementary theory should prove a sufficient explanation of what must necessarily be a most complex relationship. The most that can be said of these results is that they appear promising, and it is in the hope of stimulating further work on the lines we have indicated that they are discussed in some detail.

2. Field observations

The field observations were carried out in Freetown, Sierra Leone, during the dry season in February and March 1937. An area of 22·5 acres, defined by the ordinates of the survey map, was chosen as being a typical block of houses occupied by natives. It contained, as will be seen from the map (Fig. 1), no open spaces such as, for example, parks, railway sidings or foreshore, and was inhabited for the most part by a more intelligent type of native than other possible quarters of the town. This is an important point, since the success of an extensive trapping experiment will depend on the intelligent co-operation between assistants and inhabitants. Although the possibility of interference with the traps by the natives cannot be wholly eliminated, we consider that in the present instance this disturbing factor was reduced to a minimum.

The experiment was carried out in the following way. A plan was made and the area then divided into two roughly by the line Lewis Street—George Street West. Scattered over the half-area below the division line 35 houses were chosen from the plan, and on the first evening three traps were set in each house, left for the twelve hours of darkness and collected in the morning. The next night 35 houses in the other half were similarly treated. On the third night a return was made to the bottom half of the plan; on the fourth to the top half and so on alternately up to the sixth night. 35 new houses were trapped on each occasion and these were chosen so far as was possible adjacent to those trapped on the night when the half-area was previously visited. The buildings varied in size, ranging up to three stories, and the three traps were distributed among the various floors. There was then a pause for one night and on the eighth day the rotation of sites was restarted, wherever possible using the same houses as were trapped during the first week. If for any reason a particular house could not be revisited, an alternative one was substituted in its stead. The whole experiment lasted for a period of six weeks, and during each week 630 traps were set in 210 houses.

The traps were of the "breakback" variety, which is generally considered to be the most efficient, and only one animal could be taken in each. They were made by the French firm, "Manufactures des armes et des cycles", Loire, and consisted of two semicircles of stout wire joined across the diameter by a spring. When set a circle is formed with the bait on a trigger in the centre and the two semicircles spring together when the trigger is released. Slices of

cassava (*Manihot utilissima*) were employed as bait. The actual process of setting and collection had to be entrusted to native assistants and from D. H. S. D's. experience of them we are reasonably certain that the work was efficiently carried out. They also entered in a book the results from each house and there

Fig. 1. Map of the area trapped. (Reproduced by permission of the Director of Surveys, Freetown.)

are a few indications of possible errors in bookkeeping, e.g. rats entered as being trapped at the wrong address. This is however a small matter, as we are not concerned with the results from the individual houses, but rather with the total catch. This was checked in the laboratory where the rats were typed, sexed and so on by D. H. S. D. There remains the question of those traps, either with or without bait, which were found sprung and containing no rat or other

animal. Undoubtedly the greater proportion of these were sprung either accidentally by members of the household, stray dogs, cats, hens, etc., or by the rats themselves who managed to avoid capture: but also a number may actually have trapped rats, which were afterwards either thrown away by the inhabitants or eaten, for example, by cats. Both of these latter alternatives were reported to have occurred on three occasions during this series, and it is always possible that further instances may have been overlooked by the assistants or concealed from them by the inhabitants concerned. But such sources of error are inherent in the conditions under which this experiment was done, and provided this accidental or purposeful sabotage—if one might so term it—remains on a relatively small scale, allowance can always be made for it in the final calculations. It is most unfortunate that we have no records for this series of the number of such negative-sprung traps and, as will be seen later, we have been compelled to adopt an average figure derived from a similar type of experiment on another area in Freetown. Possibly we have painted the picture blacker than it actually was: in our judgement the figures reported in this paper were the results of efficient trapping and such errors as may have occurred were relatively unimportant.

The sum of the first two nights' results from 210 traps set in 70 houses represents the first trapping of the whole area: the sum of the third and fourth nights' the second trapping: and so on. The results are given in Table 1. The most frequent type to be captured was *Rattus rattus*; but in addition a number

Table 1

Trapping no.	Number trapped						Weekly total of		Total no. *R. rattus* trapped
	R. rattus	Other species					*R. rattus*	Other species	
		RN	*MM*	*C*	*M*	Total			
1	49	7	3	.	.	10			
2	32	4	3	.	.	7			
3	31	5	7	.	.	12	112	29	112
4	34	5	4	.	.	9			
5	16	8	1	.	.	9			
6	33	7	2	.	.	9	83	27	195
7	22	5	1	.	.	6			
8	27	4	5	.	.	9			
9	17	5	11	.	.	16	66	31	261
10	19	1	3	1	.	5			
11	18	10	3	.	1	14			
12	16	3	3	1	.	7	53	26	314
13	18	2	2	.	.	4			
14	12	1	2	.	.	3			
15	14	1	5	.	.	6	44	13	358
16	12	3	2	1	.	6			
17	17	3	2	.	.	5			
18	7	2	5	.	.	7	36	18	394

210 traps were set on each occasion.

RN = *Rattus norvegicus* *C* = *Crocidura*
MM = *Mus musculus* *M* = *Mastomys*

of traps were occupied by other species, by far the greater part being *R. norvegicus* and *Mus musculus*. From the weekly totals it is seen that these are relatively much less numerous than *Rattus rattus* and this latter type may be regarded as the principal rodent infesting this block of property. In order to avoid any misconceptions it might be as well to point out that they are not confined to the houses. A fortnight after this series was ended the area was treated with the same rotation of sites, only the traps were set in the compounds instead of in the houses. The number of traps set was 630 and 32 *rattus* were captured; a figure which agrees very well with the last weekly total for the

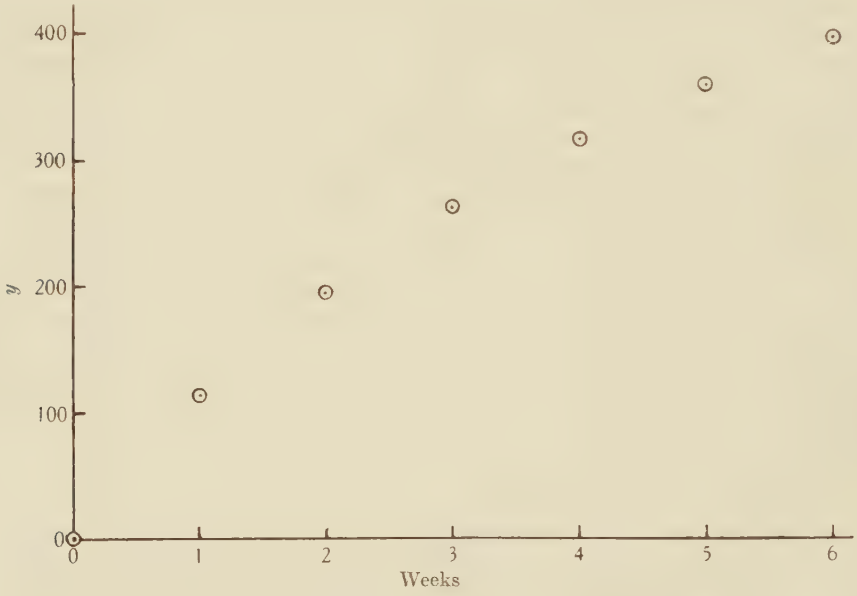

Fig. 2. The total number of *R. rattus* (y) which were trapped plotted as a function of time.

house-trapping, namely 36. The last column of Table 1 gives the total number of *rattus* trapped up to the end of each week, and when these figures are plotted as a function of time, it will be seen from Fig. 2 that they form an extraordinarily smooth curve. It was this suggestion of an underlying law and order that prompted a more detailed analysis.

3. General conceptions

Reduced to essentials, a number of animals is imagined to start their search for food at different points over an area. Supposing that in the type of animal society we are considering each individual searches independently from the others, the movements of the population may be said to be unorganized or in other words at random. During their search a certain number of traps

are encountered. This conception of a number of individuals moving over a topographic field and suffering a number of random collisions with other animals or objects in their environment, has the merits of simplicity and has been employed by many authors, e.g. Lotka (1925) and Volterra (1931), in the mathematical treatment of population questions. As Lotka (1925, p. 358) has pointed out: "we might seek to develop, for such a system, a discipline of statistical mechanics similar to that which the physicist has developed to deal with the kinetic theory of gases and allied problems."

In the type of system dealt with here, there are in reality two separate areas to consider: the area bounded by the extreme limits of the individual paths of search, within which the population may be said to be moving at random, and the area within which all the traps lie. In the case of an island, for instance, it is easy to see that the two areas can be made to coincide and the total population will then be exposed to risk. But where there are no topographical features to form a barrier to the movements of the individuals and when the same trap-boundaries are used repeatedly, the relation between the two areas becomes of some importance. The area of search for food over a period of time will depend on the habit of the species; whether it be migrant or having some fixed point such as a nest or lair to which it returns. In the case of the rat when the population is in a settled condition—neglecting, that is to say, the migratory movements which are reported to occur from time to time—the individuals leave their holes and return again to the same point or at any rate a point very close to where they started. By making the dimensions of the trap area large relative to the average radius of movement of a rat, it is thus possible to include within its bounds, as in an imaginary island, an unknown number of individuals. The overlap, which must always occur with surrounding areas, can now be considered negligible. The experience of Petrie & Todd (1923) in Egypt, where *R. rattus* were trapped alive, marked and then released, was that the movements of recaptured animals over a period of three months were limited, consisting for the most part of oscillations between two or three adjacent houses. They noted also that intensive trapping did not apparently disturb the population and that the broader streets appeared to act as a natural barrier to their movements. Although we can produce no definite measurements in support of the statement, there is no reason to suppose that the movements of *R. rattus* in Freetown were any different from those of their brethren in Egypt. This point will be returned to later in the section devoted to the arithmetical analysis of the results: for the moment it will be assumed that the furthest distance reached by any one rat during its search for food was small compared to the dimensions of the trapping area.

There is in addition another important point to be considered; whether the population at risk was distributed at random over the area. During a week 210 houses were trapped and up to three rats could be captured in each. If H = the number of houses and R – the number of *rattus* trapped during any

one week, the mean number of rats per house $= R/H = m$. Then under the hypothesis of a random distribution, the number of houses which should have 0, 1, 2 and 3 rats can be calculated by means of the successive terms

$$He^{-m}\left(1, m, \frac{m^2}{2!}, \frac{m^3}{3!}\right).$$

In Table 2 are given the number expected from this Poisson series, together with the numbers observed. The first two weeks' results are tabulated separately; while the remaining weeks have been added together in order to obtain

Table 2

No. *rattus* per house	Week 1 112 *rattus*		Week 2 83 *rattus*		Weeks 3, 4, 5 and 6 199 *rattus*	
	Obs. no. houses	Exp. no. houses	Obs. no. houses	Exp. no. houses	Obs. no. houses	Exp. no. houses
0	129	122·3	136	140·5	656	661·8
1	54	65·5	65	55·8	169	157·0
2	20	17·6	6	11·1	12	18·6
3	6	3·1	2	1·5	2	1·5
Total	209	208·5	209	208·9	839	838·9
	$\chi^2 = 3{\cdot}743$		$\chi^2 = 3{\cdot}340$		$\chi^2 = 2{\cdot}819$	
	$n - 1$		$n - 1$		$n - 1$	
	$P = <0{\cdot}10, >0{\cdot}05$		$P = <0{\cdot}10, >0{\cdot}05$		$P = <0{\cdot}10, >0{\cdot}05$	

Total $\chi^2 = 9{\cdot}902$; $n = 3$; $P = <0{\cdot}02, >0{\cdot}01$

In calculating χ^2 the 2- and 3-*rattus* houses were added together.

figures of a convenient magnitude in the 2-3-rat classes. Three houses were reported as having "rats" thrown away by the householders or eaten by cats, and since it is impossible to know whether these referred to *rattus* or *norvegicus*, they were left out of the calculations. The agreement between the expected and observed numbers is fairly close and the values of χ^2 fall just below the conventional level of $P = 0{\cdot}05$ in each of the three distributions. However when the three values are added together giving $\chi^2 = 9{\cdot}902$ and $n = 3$, $P =$ just $< 0{\cdot}02$; so that there is a suggestion of some slight disturbing influence on the random distribution. Possibly this may be due to errors of book-keeping or to the negative-sprung traps which have been previously mentioned; since for the purposes of this test we have assumed the complete efficiency of all the traps. Whatever the reason, the degree of departure from randomness is not sufficient to cause us to abandon any further application of the theory to these figures.

Lastly, there is the question of the relationship between the minimum number of hours during which every individual member of the population will have been exposed to risk and the time during which the area was trapped each night. Obviously in the design of any experiment it is desirable to have a conformity between these two times similar to that between the two areas discussed previously. Very little seems to be known about the activity of

the rat in the wild state. It has been shown by Richter (1927) that white rats in the laboratory have approximately a four-hourly rhythm of activity when food is present in the cages; when it is absent this period becomes shorter and Richter suggests that this restlessness and activity is associated with spasmodic contractions of the empty stomach. Supposing that the same conditions hold good in the field; and taking into consideration that the wild rat must search for food: then it appears a fair assumption to make that during a night every individual—apart from the young in the nests—will pass some period of time on the surface and therefore at the risk of being trapped. We are well aware that this is rather a sweeping assumption, to which a number of objections can easily be raised: but in the present state of our knowledge we submit that, for the purposes of this argument, it is good enough as a first approximation to the truth.

To summarize this section: the conception has been formed of an area being searched in a random fashion by a population which remained circumscribed over the period of the experiment owing to its habit of life. Moreover it is assumed that during any one night every individual rat inhabiting the half-area trapped will have been exposed to the risk of capture.

4. Theoretical

The area defined by the map ordinates, to which strictly speaking should be added the floor area of the second and third stories, will be regarded as a unit area and the number of hours of darkness elapsing between setting and lifting the traps as a unit of time.

Let a quantity p be defined as the probable value of the path an animal can traverse without colliding with a trap, i.e. the mean free path. Then, by the well-known theorem, the probability P that a single animal moving among a number of traps at rest will traverse a distance x without a collision, is

$$P = e^{-x/p}. \qquad \text{.....(1)}$$

Suppose that on the unit area there are T traps. Let the area be divided into T small squares, each of which on the average contains one trap. Let x be the length of the side of each of these squares; then one trap is contained in an area of x^2 and x is also the average distance between adjacent traps. It follows that $Tx^2 = 1$. Let r be the radius of the field of influence surrounding each baited trap and suppose that any animal which is within this imaginary circle will respond to the stimulus received through its senses by moving towards the centre. Then an animal may be said to have discovered or collided with any trap lying within a distance r from itself. If it moves over a distance x, which for the sake of simplicity is taken to be a straight line, it will search an area $2rx$ and will collide with any trap lying within this parallelogram. Since one trap is contained in the area x^2, the probability that there is a trap

on the area $2rx$ is $2rx/x^2$ and therefore the probability of there being no trap, i.e. no collision, is $1-2rx/x^2$. From (1)

$$e^{-x/p}=1-\frac{2r}{x},$$

or, expanding $\log_e\left(1-\frac{2r}{x}\right)$ in series,

$$\frac{x}{p}=\frac{2r}{x}+\frac{1}{2}\left(\frac{2r}{x}\right)^2+\frac{1}{3}\left(\frac{2r}{x}\right)^3+\text{etc.}$$

In the conditions of an experiment like the one we are considering, r must be small compared with the average distance between adjacent traps. It follows that $2r/x$ is a small quantity compared with unity and therefore its square, cube, etc. can be neglected. The expression above then reduces to

$$\frac{x}{p}=\frac{2r}{x},$$

and since $Tx^2=1$

$$p=\frac{1}{2rT}. \qquad \text{.....(2)}$$

Although its movement may be intermittent, an animal during a unit of time will cover a certain distance which can be termed its velocity v. The probable number of collisions which it will make is

$$\frac{v}{p}=v2rT.$$

Suppose that there are N animals on the area and that all these individuals are exposed to risk during some period of a unit of time. Now it will be very unlikely that the quantities $v_1, v_2, v_3, \ldots, v_N$ will all be the same, but it is convenient to make the simplifying assumption that they are. When in the molecular theory of gases the velocities of the individual molecules are assumed to be distributed according to the Maxwellian law, it is found that the equation defining the probable value of the mean free path differs only by a constant ($\sqrt{2}$) from that arrived at when the velocities are assumed to be the same. We can therefore say either that the N individuals move with the same velocity V; or, better, regard the quantity V as an average value defining some unknown distribution, equivalent to the Maxwellian,[1] which is assumed to be constant and independent of any factor such as the age distribution of the population. The N animals will therefore in a unit of time suffer $V2rTN$ collisions with traps.

[1] Working in two dimensions, the equivalent distribution to the Maxwellian would be that the number of animals having a velocity between v and $v+dv$ is assumed to be given by

$$dN=2Nh^2v\,e^{-h^2v^2}\,dv.$$

As a matter of interest it might be mentioned in passing that we have recently observed this distribution to be realized very closely in a similar type of problem, namely the distances, measured in a straight line, between the points at which long-tailed field-mice (*Apodemus sylvaticus*) were trapped alive and subsequently recaptured.

In general it will not be true that every collision results in the capture of an animal. Even if the traps are mechanically efficient and properly set, it may still happen that owing to the design of the trap an animal, in order to spring it, must approach in a particular way. Let c be the fraction of collisions which result in capture; then c may be called a measure of the efficiency of the traps. In future we shall employ the word "collision" in the sense of "effective collision".

Suppose for the moment that trapping is a continuous process which is not terminated at the end of each unit of time by the removal of the traps. Let y be the total number of animals trapped up to the time t and N be the initial population on the area. In addition assume that the population does not increase through young leaving the nest and immigration, or decrease through normal deaths and emigration during the time of the experiment. Then at the time t there will be $N-y$ animals and $T-y$ traps left. In the interval of time $t+dt$ the $N-y$ animals will make $cV2r\,(T-y)\,(N-y)\,dt$ collisions with the remaining traps and this quantity must equal the dy animals captured. We have, therefore, putting the constant $cV2r=s$,

$$\frac{dy}{dt}=s\,(T-y)\,(N-y), \qquad \text{.....(3)}$$

which gives on integration

$$\frac{T-y}{N-y}=\frac{T}{N}e^{-s\,(N-T)\,t}. \qquad \text{.....(4)}$$

In the case of a planned experiment, where the initial number of animals is known, this equation should express the interaction between animals and traps, if the assumptions made as to the random nature of collisions and the constant mean velocity of the individuals hold good. But in the absence of any knowledge about the value of N and given only the value of y at the end of one unit of time, as in the present series of results, little use can be made of it and we must proceed somewhat differently.[1]

In the differential equation (3) instead of the variable $(T-y)$ put $T=$ the number of traps set and keep it constant. This is the same thing as assuming that the "breakback" traps, which can catch only one individual, have become

[1] In the first part of this theory which is merely an adaptation in two dimensions of the elementary kinetic theory of gases, we have borrowed freely from various sources, e.g. Lotka (1925) and Mellor's *Higher Mathematics for Students of Physics and Chemistry*, and reference may be made to these or to any textbook of physical chemistry for further details. It should be noted that if rats be regarded as prey and traps as predators, both equations (4) and (5) can be derived immediately from the well-known Lotka-Volterra system of simultaneous equations, $dN_1/dt=(a_1-b_1N_2)\,N_1$, $dN_2/dt=(-a_2+b_2N_1)\,N_2$, where a_1, a_2, b_1, b_2 are constants and N_1 and N_2 are the number of prey and predators respectively: in the case of (4) by putting $a_1=a_2=0$ and $b_2=-b_1$; and in the case of (5) $a_1=0$, $dN_2/dt=0$. But it seemed advisable to give the development of this special case of the predator-prey relationship in full for the sake of clarity, and in order that the biological significance which is attached to the various constants may be of assistance in the design of any future experiment.

a type of cage-trap, catching any number, and that all the collisions which are made by chance with a trap already occupied result in capture. Putting $sT = k$

$$\frac{dy}{dt} = k\,(N - y),$$

whence

$$y = N\,(1 - e^{-kt}). \qquad \text{.....(5)}$$

It follows from this equation that during one unit of time there would occur $N\,(1 - e^{-k})$ collisions and this quantity would represent the number trapped if all the collisions were able to take place. Let

$$1 - e^{-k} = k'.$$

The average number of collisions per trap is $k'N/T$ and, since it has been assumed that the collisions take place at random, it follows from the Poisson distribution that the proportion of traps which suffer 0, 1, 2, etc. collisions will be given by

$$e^{-k'N/T}, \quad \frac{k'N}{T}e^{-k'N/T}, \quad \frac{1}{2!}\left(\frac{k'N}{T}\right)^2 e^{-k'N/T}, \text{ etc.}$$

The first collision results in the trapping of an animal and any second or more collisions on that trap are ineffective. Those animals which might have been captured at this point are therefore free to collide with other unoccupied traps. But if $k'N < T$, the proportion of traps which would be expected to suffer two or more collisions is small compared with the proportion which suffer none or only one: therefore the number of animals which collides by chance with an occupied trap is small and the possibility that these animals manage to collide with unoccupied traps during the time left to them, might be considered negligible. An imaginary numerical example will perhaps make this point clear. If $k'N/T = 0{\cdot}281$ and $T = 200$, the expected number of traps which will suffer no collision is 151·0; one collision, 42·4; two collisions, 6·0; and three collisions, 0·6. Had all these resulted in capture we should have expected 56 animals to have been trapped; actually only 49 could have been owing to the type of trap. There were therefore seven animals which during the course of the night collided with traps already occupied and were then free to make contact with the remaining unoccupied ones. If we assume, taking into account their velocity and the average distance between traps, that it is very unlikely that they will have managed to do so during the time left before the night's experiment was ended, then, putting R = the number of *rattus* captured, the proportion of unoccupied traps,

$$\frac{T - R}{T} = e^{-k'N/T}. \qquad \text{.....(6)}$$

With regard to the present experiment there are two further complications which have to be taken into account: a certain number of traps were occupied

by other species and others were found sprung and containing no animal in the morning. Both these factors act in the same way by preventing *rattus* being caught by these particular traps. Apart from those which actually caught *rattus*, the initial number of traps (T) is being decreased throughout any one night by the action of these outside agencies. Let b equal the number of traps occupied by other species and found negatively sprung; then provided that b be relatively small compared with T, it will be sufficiently accurate for our purpose to assume that the number of traps set, which we have taken as constant in equation (5), can be described by a decreasing linear function of time, say $T-bt$. It follows that the average number of traps per unit time which are free to catch *rattus* is $T-b/2$. Let $b/2=n$: then had there been only *rattus* present on the area and no negative sprung traps, we should have expected the n traps to have caught the same proportion as the $T-n$, i.e. $nR/T-n$. For instance on the first trapping of the area, $T=210$, $n=26$ and 49 *rattus* were trapped; $49/184=0{\cdot}2663$ and we should have expected $26\times 0{\cdot}2663$, say approximately seven *rattus* to have been caught in the 26 traps. We can apply to these individuals the same arguments used in the case of those rats which collided with traps already occupied by their own species. The proportion of traps unoccupied by *rattus* is $T-n-R/T-n$ and from (6)

$$T\{\log_e(T-n)-\log_e(T-n-R)\}=k'N. \qquad \ldots\ldots(7)$$

It will be seen from the foregoing argument that this equation can hold good only in certain limited conditions. In the first place, the type of trap which is commonly employed as being the most efficient and which can only catch one individual, raises a number of grave difficulties. It might be suggested that it is only when $k'N/T$ is a relatively small quantity, e.g. $<0{\cdot}4$ or $0{\cdot}5$, that it is justifiable to assume the improbability of the individuals who collided with occupied traps, being able to collide with other, unoccupied ones during their remaining search for food. These figures are equivalent to 67–60 % of traps remaining unoccupied and any experiment giving a lower percentage would be suspect. But it is impossible to be dogmatic on this point in the present state of our knowledge and these suggestions must be taken as merely tentative. Lastly the species trapped must be either the only or at least the preponderating type on the area. If the number of traps occupied by other species becomes relatively large, or several species are caught in approximately equal numbers, the conditions are changed and the problem becomes one of the competition for traps between two or more populations, each having different velocities.

5. Arithmetical analysis

The highest value of $k'N/T$ which these results gave was 0·3097 and *R. rattus* was the preponderating type on the area: we shall conclude therefore that a quantity, which was proportional to the population each time the area was trapped, can be calculated by means of the expression

$$T\{\log_e(T-n)-\log_e(T-n-R)\}.$$

It follows that if a suitable function to describe the population can be found, it should be possible to calculate a value for k'. Apart from the loss due to trapping, the population will lose in numbers through the normal death-rate and emigration; and it will gain through immigration from sources outside the area and also the number of young leaving the nest to enter the population at risk. So far as our observations went, the rats of Freetown as a whole showed no violent fluctuations in numbers: it appeared a relatively stable population. Since this experiment lasted for only six weeks, the simplest assumption to make is that during this period immigration and young recruits balanced on the average the loss due to emigration and normal deaths. Then if N_0 be the original number of *rattus* on the area and y the total number trapped up to any particular time t

$$N_t = N_0 - y_t,$$

and therefore from (7), putting

$$T\{\log_e(T-n)-\log_e(T-n-R)\}=z, \qquad \text{.....(8)}$$

$$z = k'N_0 - k'y.$$

That is to say, the values of z should fall on a straight line when plotted against the values of y; $k'N_0$ being the value of z when $y=0$, and k' being the tangent of the angle which the line makes with the y axis. The next step is to fit a straight regression line to the data and to test its goodness of fit by the customary statistical methods. In doing so, we are testing not only whether the assumption of a balanced population is correct, but also the validity of the various assumptions made in section 3. If any one or all of these were to fail, we should expect either that the points of z would fall on a curve relative to the y axis or that no simple functional relationship between z and y could be established.

In calculating the values of z from the observed data by means of equation (8), it is unfortunate, as was mentioned in a previous section, that no figures are available for the number of negative-sprung traps. On another area in Freetown, which was trapped in a similar fashion to the present one, it was observed that in one week during which 630 traps were set overnight, 128 or 20·3 % were found in the morning sprung and containing no rat or other animal. We have assumed this to be an average figure which might be expected in a trapping experiment done under similar urban conditions. The estimate of n for each trapping is thus half the sum of 42 plus the number of traps

observed which were occupied by other species. The estimates of z being made from the proportion of unoccupied traps are subject to large sampling errors (Greenwood & Yule, 1917; Fisher, 1935) and therefore a considerable scatter of the observations will be expected in the graph (see Fig. 3). The sampling variance of an estimate of z is given by

$$\sigma_z^2 = \frac{T^2 R}{(T-n)(T-n-R)},$$

and the square root of this quantity is the standard error. In columns 4 and 5 of Table 3 are given the values of $z \pm$ S.E. derived from the data together with those calculated from the regression line, fitted by the Method of Least Squares,

$$z = 51{\cdot}26737 - 0{\cdot}105642\, y.$$

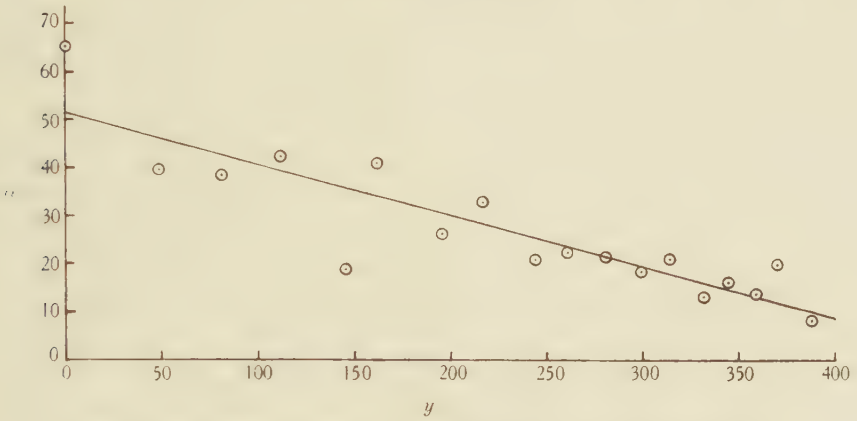

Fig. 3. The observed values of z plotted against y. The equation for the straight line is $z = 51{\cdot}26737 - 0{\cdot}105642y$.

The mean sampling variance of the values of z calculated from the observations can be used as a test for the goodness of fit of the regression line, by comparing it with the mean square deviation of the observed values from those calculated by means of the equation. For if the departure from linearity is at all marked, the mean square deviation from the regression line will be significantly greater than the mean variance expected from the errors of random sampling. The mean variance of the 18 values of z is 33·2269 and the sum of the squares of the deviations of the observed values from those calculated by means of the equation, is 735·47669. Since two constants have been calculated from the data, $18-2=16$ degrees of freedom are left and thus the mean square deviation from the regression line is 45·9673. If the estimate of the mean variance of the observed values of z were exact, we could test by means of

$$\chi^2 = \frac{45{\cdot}9673}{16 \quad 33{\cdot}2269},$$

whence

$$\chi^2 = 22{\cdot}13.$$

Table 3

Trapping no.	$T-n$	y	Observed $z \pm$ S.E.	Calculated z	Expected no. *rattus* trapped	Observed no. *rattus* trapped $= R$
1	184	0	65·03 ± 9·33	51·267	39·9	49
2	185	49	39·88 ± 7·06	46·091	36·5	32
3	183	81	38·98 ± 7·01	42·710	33·7	31
4	185	112	42·65 ± 7·33	39·435	31·7	34
5	184	146	19·10 ± 4·78	35·844	28·9	16
6	185	162	41·26 ± 7·19	34·153	27·8	33
7	186	195	26·43 ± 5·64	30·667	25·3	22
8	184	217	33·32 ± 6·42	28·343	23·2	27
9	181	244	20·71 ± 5·03	25·491	20·7	17
10	187	261	22·50 ± 5·16	23·695	20·0	19
11	182	280	21·87 ± 5·16	21·688	17·9	18
12	185	298	19·00 ± 4·75	19·786	16·6	16
13	187	314	21·25 ± 5·01	18·096	15·4	18
14	188	332	13·85 ± 4·00	16·194	13·9	12
15	186	344	16·43 ± 4·39	14·927	12·8	14
16	186	358	14·01 ± 4·04	13·447	11·5	12
17	187	370	20·02 ± 4·86	12·180	10·5	17
18	185	387	8·10 ± 3·06	10·384	8·9	7
Total					395·2	394

y = Total number of *R. rattus* caught up to the time of each trapping.
$z = 210 \{\log_e (T-n) - \log_e (T-n-R)\}$

$\chi^2 = 16{\cdot}792$
$n = 16$
$P = <0{\cdot}50, >0{\cdot}30$

For 16 degrees of freedom, $P = <0{\cdot}20, >0{\cdot}10$ or in other words a value of χ^2 as large as 22·13 would be expected in about 10 % of such cases. Since the mean variance also has a sampling error, there is really nothing in it and the straight regression line gives a perfectly satisfactory fit to the data.

In columns 6 and 7 of Table 3 are given the observed number of *rattus* caught at each trapping of the area, together with the number expected from theory. These latter figures, allowing for the same number of traps occupied by other species and negatively sprung, are calculated from the values of z in column 5 by means of the expression

$$\text{Expected number of } rattus = (T-n)\,(1-e^{-z/T}).$$

The agreement is very good indeed; $\chi^2 = 16{\cdot}792$ and for 16 degrees of freedom P lies between 0·30–0·50. As judged by these statistical tests, there is nothing in this data which is inconsistent with the various assumptions made during the course of the argument. Whether they are sufficient remains to be seen from further work on the lines indicated in the introduction to this paper.

An estimate can now be made of the two unknown constants, N_0 and $s = cV2r$. The calculated value of $k' = 0{\cdot}105642$; $k'N_0 = 51{\cdot}26737$ and therefore the probable number of *rattus* on the area at the start of the experiment was

$$N_0 = 485.$$

Since $k' = 1-e^{-k}$, $k = 0{\cdot}111649$; the number of traps set was 210 and since $k = sT$

$$s = 0{\cdot}00053166.$$

As a check on the number of *rattus* which should have been caught during each unit of time, it is now interesting to use equation (4) when $t=1$, i.e.

$$\frac{T-y}{N-y}=\frac{T}{N}e^{-s(N-T)}.$$

The average number of traps which could catch *rattus* during any particular unit of time, namely $T-n$, is used in this equation instead of the actual number set (T). For the first trapping of the area, $T-n=184$; inserting this together with the above values of N_0 and s, and solving for y, the expected number of *rattus* = 40·2. Actually 49 were trapped; so that at the time of the second trapping $N=485-49=436$; $T-n=185$, whence $y=36{\cdot}8$. The calculation can be carried out in a similar fashion for the remaining 16 trappings. As shown in Table 3, the expected numbers calculated by the previous method for the first and second trappings were 39·9 and 36·5 respectively, so the agreement is very close indeed.

The last step is to estimate the errors which must be attributed to the calculated values of N_0 and s. If Z be the value calculated by means of the regression line for any particular value of y and z be the observed value, then the mean square deviation from the regression line, n being the number of observations and S the symbol for summation, is

$$\sigma^2=\frac{S(z-Z)^2}{n-2}=45{\cdot}967293. \qquad \text{.....(9)}$$

Then the variance (V) of k' is given by

$$V(k')=\frac{\sigma^2}{S(y-\bar{y})^2},$$

where $\bar{y}$ is the arithmetic mean of the values of y. The square root of this quantity is the standard error of k' and was found to be 0·014009. Then since

$$1-k'=e^{-k},$$

it can be shown that $$V(k)=\frac{1}{(1-k')^2}V(k'),$$

whence the standard error of $k=0{\cdot}015664$. Since $k=sT$ and $T=210$ is known exactly

$$s=0{\cdot}00053166\pm 0{\cdot}00007459.$$

We are greatly indebted to Dr J. O. Irwin for showing us how to arrive at the error of N_0. Write the equation for the straight line in the form of $z=\bar{z}-k'(y-\bar{y})$, where $\bar{z}$ and $\bar{y}$ are the means of the observed values of z and y respectively. Since $k'N_0$ is the value of z when $y=0$

$$k'N_0=z+k'\bar{y},$$

$$N_0=\frac{z}{k'}+\bar{y}.$$

Whence $$V(N_0) = V\left(\frac{\bar{z}}{k'}\right) = \frac{V(\bar{z})}{k'^2} + \frac{\bar{z}^2 V(k')}{k'^4}$$

or $$V(N_0) = \frac{\sigma^2}{k'^2}\left\{\frac{1}{n} + \frac{\bar{z}^2}{k'^2 S(y-\bar{y})^2}\right\},$$

where σ^2 is given by equation (9) above and n is the number of observations (18). Calculating this quantity and taking the square root, we have

$$N_0 = 485 \pm 37.$$

Now we might wish to test whether this estimated number of *rattus* is significantly different from some hypothetical number N'. The hypothesis to be tested is that the deviation $485 - N'$ is distributed normally about zero with a standard deviation of 37, which estimate is based on 16 degrees of freedom. Using "Student's" t test (Fisher, 1935)

$$t = \frac{485 - N'}{37}.$$

From the tables of the distribution of t, for 16 degrees of freedom t has a 5 % chance of lying outside the limits $\pm 2{\cdot}12$. Inserting this value of t in the equation

$$N' = 485 \pm 78.$$

Thus we can say that, assuming the validity of this theory of trapping, the fiducial probability is 95 % that there were between 407 and 563 *R. rattus* on the area at the time when the experiment was started.

6. Discussion

It is an interesting speculation to carry this elementary theory a step further. In the constant $s = cV2r$, the fraction c and the quantity $2r$ refer to the properties of the traps and provided that the type of trap and the method of baiting are unchanged, they can be taken as constant in all such experiments. The quantity V is, however, more complex. We have tended to assume that it is dictated by the food-requirements of the animal. But it is clear that it refers to all the causes of activity on the surface and thus may vary from experiment to experiment, not only with regard to the difficulty of obtaining food at different seasons or on different areas, but also on account of other factors, such as, for instance, the particular species having an increased activity during the mating season. But it is possible to imagine certain conditions, for example a contemporary series of experiments, in which we might feel justified in assuming that V for some particular species could be taken as being approximately of the same relative magnitude on all the areas trapped. Then using the same type of trap and the same unit of trapping time—the latter is a convenience rather than a necessity—and having an estimate of

the value of $cV2r$ from a series of trappings on some unit area, it is theoretically possible to calculate the probable population on another area which has only been trapped once—an immense saving of labour. Any difference in the size of the areas requires an adjustment in the value of $cV2r$, since its essential constituent $V2r$, or the mean area traversed during a unit of time by an individual, is expressed in terms of the unit area. If a_1 be the size of the latter, a_2 the size of any other area and T the number of traps set, then $cV2rTa_1/a_2 = k$: since we have an estimate of the error of $cV2r$, it is therefore possible to find the value of $k' \pm$ S.E. which will apply to the second area. From the proportion of unoccupied traps z is calculated together with its sampling error and z/k' is then the probable population on the area. The error of this estimate, where σ_2 and $\sigma_{k'}$ are the errors of z and k' respectively, is given by

$$\sigma_N = \pm \frac{1}{k'} \sqrt{\left\{ \left(\frac{z\sigma_{k'}}{k'} \right)^2 + \sigma_z^2 \right\}}.$$

These errors are relatively very great: as an example suppose another area, which will be taken as being of the same size as our unit area for the sake of simplicity, had 210 traps set of which 50 were found to have caught *rattus* and $n = 0$. Then

$$N = \frac{57{\cdot}1061 \pm 8{\cdot}1009}{0{\cdot}105642 \pm 0{\cdot}014009}$$

$$= 541 \pm 105.$$

The percentage error is 19·4 compared with 7·6 which was obtained for the probable population on the unit area: the reason being that the latter is an average figure to the accuracy of which each of the 18 trappings has contributed its quotum of information. In the case of the single trapping, even if k' were known exactly, we would have $N = 541 \pm 77$; that is to say, more than two-thirds of the total error is due to the sampling errors involved in an estimate made from the proportion of unoccupied traps. The degree of accuracy which is obtained at any particular level of proportionality, depends on the number of traps set. Suppose that 50 traps had been set on another area and that $a_1/a_2 = 4{\cdot}2$, $n = 0$; then k' still has the same value. If 12 *rattus* were trapped—approximately the same proportion of unoccupied traps as in the previous example and also for the first trapping on our unit area—$z = 13{\cdot}7218 \pm 3{\cdot}9736$, $N = 130 \pm 41$ and the percentage error has risen to 31·5. With increasing proportions of unoccupied traps it rises still higher; for example with 88 % of traps unoccupied and 50 traps set, $z = 6{\cdot}3917 \pm 2{\cdot}6112$ and $N = 61 \pm 26$ or a 42·6 % error. These considerations affect not only this somewhat speculative application of an estimated value of $cV2r$ to the results from a single trapping, but also the analysis of any experiment designed on the same lines as that in Freetown. If this latter had been carried out on the scale of 50 traps to approximately 5 acres, it is very doubtful whether we

would have been able to establish any agreement between the observed results and those expected from theory.

There is, however, an improvement in the design of such experiments which follows logically from the argument and which would appear well worth the trouble of investigating. In discussing the employment of the single trap we have already touched upon the limitations which this imposes on the values of $k'N/T$. It is true that the latter can always be adjusted to the requisite magnitude either by increasing the number of traps or by leaving them in contact with the population for a shorter period of time. But if, instead of there being one trap at a certain point on the area, a group of three or four traps be set together at the same point, thus forming a trap-unit, many of the difficulties disappear. Theoretically this would permit of a wider range of values for $k'N/T$ giving consistent results, since up to three or four collisions with a trap-unit can now result in capture. Moreover, if the values of $k'N/T$ be such that the probability of there being more collisions than there are traps in the unit is very small indeed, then the conditions symbolized in equation (5) are realised and it follows that the number of animals trapped during a unit of time is proportional to the population or $R = k'N$. The estimate of $k'N$ is now based on a count of a definite number of individuals: a more satisfactory estimate than the less precise one derived from the proportion of unoccupied traps.

Finally it may be suggested that, if the purpose of a trapping experiment be to determine the density of a species at some particular time, it is somewhat unsatisfactory to adopt a method which involves the destruction of a greater part of the population. A system of live-trapping and marking is ecologically much sounder. It is to be hoped that the technique of this type of experiment can be developed along the lines suggested in the preceding paragraph, so that all the effective collisions with a live-trap unit result in capture. Then to take the simplest example of a constant population over the time of the experiment, if every animal captured be marked and released, the total number marked (m) up to the time of any particular trapping is known. Assuming that no deaths occur among the marked individuals and that both marked and unmarked are trapped with equal ease, the number unmarked is $N_0 - m$; then if u be the number of the latter caught at any trapping, $u = k'N_0 - k'm$; and the results are thus susceptible to the same type of arithmetical analysis as used in the present instance. But it is useless entering into details in the absence of any data and this is only a rough sketch of the type of experiment we have in mind. Moreover, further work on this trap-animal reaction may well show that the theory requires a more complicated mathematical treatment than the one employed here as a first approximation.

7. Summary

The results from a series of trappings, all done on the same area in Freetown, Sierra Leone, have been analysed in the light of a theory of trapping, which is merely an adaptation of the elementary kinetic theory of gases. The development of this theory is given in full and the arithmetical analysis of the results has revealed nothing which is inconsistent with the fundamental hypothesis. The probable number of *R. rattus* on this area has been calculated and the errors involved in this type of estimate are discussed, leading to certain suggestions for the design of such experiments in the future.

8. Acknowledgements

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HABITAT SELECTION AMONG BIRDS IN A LAPLAND BIRCH WOOD

By H. N. SOUTHERN and L. S. V. VENABLES

(*With Plates* 4–6)

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1. Introduction

The following notes are a summary of information gathered from field work during two summers in Swedish Lapland. The area worked each time was the basin of the Abiskojokk river, which flows into Lake Torne Träsk near Abisko (Lat. 68° 12′ N., Long. 18° 20′ E.). In neither season were censuses carried out, and the aim of the paper is rather to demonstrate what is the distribution of the bird population in relation to the vegetation of the habitats, and what factors govern the choice of such habitats. It is also proposed to deal briefly with the effect of such habitat selection upon the time of laying of the various species. In 1936 the field work was done during early and mid June by the second author in collaboration with Mr W. H. Thompson; in 1937 from mid June to mid July by the first author in collaboration with Mr W. A. S. Lewis.

We do not propose to restate the theory of habitat selection advanced by Lack (1933), but the field work was done with his ideas in mind, so that it is to a certain extent explanatory of them. Both in the table and in the notes on species it has been assumed that direct limiting factors and indirect ones (via the psychological preferences of the bird) have equal value in determining distribution.

2. Description of the habitats

(*a*) *General considerations*

A brief survey of the major vegetation groups into which this area falls has already been published (Southern & Lewis, 1938). Birch forest (*Betula alba* and many subspecies) occurs in all the river valleys and in this locality

Phot. H. N. Southern and W. A. S. Lewis

Phot. 1. Tributary of the Abiskojokk with silver birch woods on either bank, showing one of the few clumps of conifers.

Phot. H. N. Southern and W. A. S. Lewis

Phot. 2. The three major types of habitat in Swedish Lapland: (1) swamp edge with willow, (2) birch woods, and beyond that (3) treeless fells.

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extends from 1000 ft. (the height above sea level of Lake Torne Träsk) to about 2500 ft. The tree line is of course much less clearly defined on the more gradual slopes. On the steeper mountain sides there is no dwindling down to scrub, but the last trees are large ones, such as can resist the scouring snow movements, which occur every spring. Thus there is a sharp line marking off the forest avifauna from that of the fells.

The conformation of the land and the snow melt govern the distribution of the major habitats, since, when the latter forms a well-marked canal, which continues to carry down water from the mountains long after the birch woods themselves are clear of snow, the ground remains exceedingly wet; thus a chain of swamps is formed wherever there are slight pockets in the ground and the trees have little chance of spreading in here. Changes of vegetation take place with the alteration of water courses, and in places large numbers of dying birch trees were seen standing in a marshy area, while colonization was taking place in others.

The snow melt is a most important factor in governing the commencement of breeding of birds. Thus hole-nesting species will be able to start much earlier than ground-nesting ones, since the latter must wait not only for the snow melt, but for the drying of the ground. Since this occurs patchily, commencement of breeding is spread over a longer time than with hole or tree nesting species.

(*b*) *The subdivisions of birch forest*

Roughly these may be given as:

A. Birch forest with good undergrowth.
B. Birch forest with poor undergrowth.
C. Birch scrub with good undergrowth.
D. Birch scrub with poor undergrowth.
E. Swamp edge.

Type A of course contains the largest trees of all, and in this habitat come the small clumps of conifers (*Pinus sylvestris* var. *lapponica*) which crop up only occasionally as far north as this. The effect upon the avifauna however is noticeable. All the larger birds nest in these for preference, e.g. hooded crows, merlins, ospreys (*Pandion haliaetus*), rough-legged buzzards (though most of these last are out on the fells), and even fieldfares and bullfinches (*Pyrrhula p. pyrrhula*). In addition a pair of non-breeding waxwings (*Bombycilla garrulus*) was seen in 1936 in the conifer areas. The earlier party also saw old nesting sites of black woodpeckers (*Dryocopus martius*), which are probably limited to these trees, since no birch would be large enough to accommodate them.

Much of the birch forest of types A and B was closed, though large areas of open formation were present, these being inhabited especially by flycatchers and redstarts. Some parts naturally were intermediate between the two types. Other trees also occurred, such as bird cherry (*Prunus padus*), some Salices

(though these were mostly in the swamps), and some poplars (*Populus*). These however could have had little effect upon the bird distribution. The birches in A and B were mostly about 20–25 ft. high, though 30 ft. was not an uncommon size; in C and D the scrub was generally dense and ranged up to 12 ft. in height with isolated larger trees in places.

In A and C the secondary growth was remarkably dense and the following plants were co-dominant: *Empetrum nigrum*, *Vaccinium vitis-idaea*, *Juniperus communis var. nana*, *Phyllodoce coerulea*, *Cassiope tetragona* and *Betula nana*. In B and D much the same plants were present but the dryness of the ground made them much sparser. Most of the vegetation occurs upon fairly dry ground, off which the snow melt drains early. In wetter parts swamp vegetation appears; *Trollius europaeus*, *Viola biflora*, etc., and the type of habitat may be then classed as verging towards E.

Exposure is also a factor to be reckoned with: most of the lakeside conformed to type A, but one headland, which was very windswept, approximated more to type C. On the whole, however, the dampness of the ground was the chief determining factor.

3. The avifauna

The distribution of the various species is given in the table. The following notes on some of them are appended.

(1) *Brambling*, *mealy redpoll* and *willow warbler*. These three species may be reckoned as the most adaptable since two of them are found in all five habitats and the third in all but swamp edge. The mealy redpoll and willow warbler even extend into areas up on the fells which cannot even be classed as scrub, the former nesting, when necessary, on the ground, the latter occupying any small clump of bushes, provided that a song-post 6–8 ft. high is present. This limitation in the willow warbler's case is again seen in type E habitat, where it will nest away from the trees in clumps among the marshes, but still sings from the nearest forest edge. It is even able to overcome nesting difficulties presented by lack of undergrowth, and in 1937 two nests were discovered built quite openly of conspicuous grasses in 3 in. *Vaccinium*.

(2) *Woodpeckers* and *tits*. The former are only found in types A and C, because they are unable to adapt themselves to the small trunks of the birches in scrub areas. Willow tits inhabit chiefly swamp edges and the damper parts of A, because they must have decaying trees in which the excavation of nest holes is easy.

(3) *Fieldfare* and *redwing*. These are also confined to A and B by nesting requirements and also by the necessity for a song-post. The redwing may nest on the ground and still need a tree from which to sing. The fieldfare is much more a colonial nester and new nests are generally found close to those of the previous year, which last very well, since they are constructed of mud and kept in cold storage all winter.

Phot. H. N. Southern

Redwing (*Turdus musicus*) nesting on the ground. The ground vegetation is typical of fairly open birch wood, consisting largely of *Vaccinium* and *Empetrum*.

Distribution of birds in subarctic birch wood

A = wood with good undergrowth. C = scrub with good undergrowth.
B = wood with poor undergrowth. D = scrub with poor undergrowth.
E = swamp edge.

Species	A	B	C	D	E	Special features	Date of first egg
Hooded crow (*Corvus c. cornix*)	×	×	·	·	·	Tall tree for nesting	May
Magpie (*Pica p. pica*)	×	×	·	·	·		May
Mealy redpoll (*Carduelis f. flammea*	×	×	×	×	×	Nest in fork at any height or even built on the ground. *Salix* fluff for nest material	24 July
Pine grosbeak (*Pinicola e. enucleator*)	·	×	·	·	·		—
Brambling (*Fringilla montifringilla*)	×	×	×	×	·	Nest in fork at any height, but generally high	10 June–1 July
N. willow tit (*Parus atricapillus borealis*)	×	×	·	·	×	Large stump for nesting. Most at or near marsh	28 May
Spotted flycatcher (*Muscicapa s. striata*)	×	×	·	·	·	Open formation for "snapping" method of feeding. Nest often in broken-off birch stump	14 June
Pied flycatcher (*Muscicapa h. hypoleuca*)	×	×	·	·	·	Open formation or wood edge for "pouncing" method of feeding. Song-post. Nest holes not in C and D	12 June
N. willow warbler (*Phylloscopus trochilus acredula*)	×	×	×	×	×	Some undergrowth under which to conceal nest. Song-post. Usually least common in D on account of exposure	14–25 June
Garden warbler (*Sylvia borin*)	×	·	×	·	·	Tall, dense undergrowth for nesting	Arrival 25 June
Redwing (*Turdus musicus*)	×	×	·	·	·	Tall song-post. If a ground nester, some undergrowth in which to conceal nest	20 May and 23 June
Fieldfare (*Turdus pilaris*)	×	×	·	·	·	Tall song-post. Fork for nest at any height	28 May and 1 July
Redstart (*Phoenicurus p. phoenicurus*)	×	×	·	·	·	Same as for pied flycatcher	12 June
Arctic bluethroat (*Luscinia suecica*)	×	·	×	·	×	Confined to formations with undergrowth for nesting place	8 June
Dunnock (*Prunella m. modularis*)	×	·	·	·	·	Tall, dense undergrowth for nesting	—
Three-toed woodpecker (*Picoides tridactylus*)	×	×	·	·	·	Open formation where the largest trunks are	17 May
N. lesser spotted woodpecker (*Dryobates m. minor*)	×	×	·	·	·		18 May
Merlin (*Falco columbarius aesalon*)	×	×	·	·	·	Tall tree for nesting	June
Rough-legged buzzard (*Buteo l. lagopus*)	×	·	·	·	·		16 May
Willow grouse (*Lagopus l. lagopus*)	×	·	×	·	·	Undergrowth for nesting.	3–10 June
Total species	20	15	6	3	4		

(4) *Garden warbler* and *dunnock*. Both these species are uncommon and only found in the densest parts of habitat A. Thus they are among the least adaptable of the birch wood birds.

(5) *Bluethroat*. This species shows a marked preference for type C and will sing from almost any height, so long as it is sufficiently conspicuous. Along the railway a favourite song-post was on the electric cables. Nesting limitations confine it to areas with good undergrowth.

(6) *Flycatchers* and *redstart*. These are subject to roughly the same nesting limitations as the woodpeckers, but their mode of feeding further confines them to places where the formation is open. Song is uttered from among the trees and not necessarily from conspicuous branches, though no doubt scrub would be too dense for this purpose.

In general it may be seen that the birds may be classified in this way according to their adaptability. Thus the most adaptable may be said to be the commonest species, and the fall-off in the number of habitats occupied is generally accompanied by a decline in absolute numbers of the birds. Exceptions to this are the woodpeckers, which are not at all common, while the bluethroat is locally very abundant, when the type of ground is suitable. However, the numbers and ubiquity of such species as mealy redpoll and brambling are remarkable.

4. Effect upon commencement of breeding

The dates given in the right-hand column of the table are all taken from 1937, when considerably more nests were found. In many cases they are approximate, having been worked out from the time of hatching or fledging, but it is probable that they are correct enough to a few days. It should be pointed out that the spring in 1937 was an exceptionally early one, so that the dates are only valuable relatively to one another. Two points should especially be noticed.

(1) The habitat selection of the bird largely determines the extent to which the onset of breeding is affected by the snow melt. Thus all the species that nest in trees, either in the branches or in holes, can start considerably earlier than ground nesters. Woodpeckers, tits and the larger tree-nesting species, such as the rough-legged buzzard, hooded crow and magpie, all started about the middle of May, and they are followed shortly towards the end of the month by the fieldfares and redwings. In early June these are followed by other tree-nesters, such as the brambling and redstart. Of those which lag behind the mealy redpoll seems to be limited by a supply of *Salix* fluff, with which the nest is invariably lined. This may not be quite such an arbitrary habit as it sounds, since the white colour of the nest lining may counteract the ill effects of excessive heat upon the nestlings and influence chick mortality, as Linsdale (1936) found in the case of some American birds. The flycatchers are noticeably

Phot. H. N. Southern

Phot. 1. Three-toed woodpecker, ♀ (*Picoides tridactylus*), one of the early nesters, using the larger birches for nesting sites.

Phot. H. N. Southern

Phot. 2. Mealy redpoll, ♀ (*Carduelis f. flammea*), a late nester, using birches of all sizes.

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late arrivals in Britain, and this lateness may be correlated with the amount of insect prey upon the wing.

The earliest of the ground nesters are the bluethroat and the willow grouse and they are probably inclined to occupy the areas of wood that dry up first. After these comes the willow warbler, and the series can be continued by including the swamp nesters, all of which are comparatively late.

(2) Among the species which are directly influenced in nesting by the state of the ground, considerable variation in the date of breeding onset is noted. This is no doubt correlated with the different speeds at which areas dry off after the snow melt. Lack (1933) found a similar case in the Arctic terns (*Sterna macrura*) on Bear Island. Both willow warbler and willow grouse show this variation, though it is only fair to add that so does the brambling. Further evidence is again shown by swamp and fell species; meadow pipit (*Anthus pratensis*) nests were found in 1937 in all possible stages, while the same applied in a less degree to reed bunting (*Emberiza s. schoeniclus*) wheatear (*Oenanthe oe. oenanthe*) and snow bunting (*Plectrophenax nivalis*).

In conclusion the authors wish to point out that although the last part of this paper is considered most suggestive, it would be much strengthened by any further data that future workers in this area may obtain.

5. Summary

1. Observations on the habitat selection of birds in a subarctic birch wood were made in 1936 and 1937.

2. The major habitats are defined and the subdivisions of birch wood indicated.

3. The types of habitat favoured by each species are given and the limiting factors noted.

4. From these data it is shown that, roughly speaking, the most adaptable species are the commonest.

5. Dates of the onset of breeding are correlated with the type of habitat, through the influence on the latter of the date of snow melting.

6. Ground nesters therefore show more variation in this date, since the ground dries unevenly.

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STUDIES OF THE SOIL FAUNA, WITH SPECIAL REFERENCE TO THE RECOLONIZATION OF STERILIZED SOIL

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(*With Plate 7 and 12 Figures in the Text*)

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1. Introduction

The present investigation was designed primarily to supply information on the recolonization of sterilized soil by soil macro-organisms. Soil sterilization is commonly practised in glasshouse horticulture for restoring the fertility of the soil and the destruction of the noxious animals; but a perusal of the literature revealed the fact that no evidence was available concerning the recolonization of the sterilized soil by such animals.

The work was undertaken at the suggestion of Dr C. B. Williams and was carried out from November 1935 to March 1937 at Rothamsted Experimental Station, Harpenden.

Advantage was taken of the fact that a new machine for isolating soil fauna had been recently designed by Ladell (1936). This apparatus, by means of which the fauna is floated out of the soil, has been used throughout the investigation.

The term soil fauna is used to include all the macro-organisms which at one time or the other in the course of their development from egg to the adult stage, spend a part or whole of their life time beneath the surface of the soil. According to this definition they may be permanent denizens of the soil or temporary visitors for the purpose of food, shelter, etc.

2. Review of previous work

The earliest attempt to study the soil fauna was in Europe by Diem (1903), followed by Holdaus (1910) who published brief records of the soil organisms. American zoologists followed suit and took up the study of the ecological relationship of insects and other invertebrates. McAtee (1907) made a preliminary start by examining an area of 4 sq. ft. of the forest floor and the grassy meadow at Washington for insects and seeds in order to study their relationship to the bird food. He computed 1·2 million invertebrates per acre for the former and 13·7 million for the latter habitat. Comprehensive insect surveys were soon after organized to preserve for the future a record of the fauna of some of the American States in transformation from wilderness to agricultural and industrial countries. The work of Shelford (1913), Vestal (1913) and Adams (1915) is of great significance in this connexion.

More intensive types of investigations were also undertaken at this time in England and some useful information obtained. It was found that, owing to the continuous changes brought about by cultivation, soil insects were not homogeneous in distribution except to some slight extent in grassland, but that even there the composition was considerably affected by the migration of the insects to and from the arable lands. The first soil insect survey was carried out by Cameron (1913) at Manchester, where he recorded 163 species, the majority of them surface forms. He dealt with an area which was not uniform and possessed heterogeneous vegetation. His second paper (1917) deals with similar investigations of two types of grassland in Cheshire. The difference in

fauna which he observed in these areas was attributed to the different environmental conditions. Buckle (1921) working at the same place concluded a little later that the distribution and numbers of the soil fauna were more stable on grassland than on arable land; that the fauna increased in both with the growth of vegetation, and that there was no characteristic fauna of arable land. Morris (1920) made a study of a permanent pasture, also in Cheshire, and estimated a population of 3·6 millions per acre, Coleoptera predominating in number of species. He also found that the factors influencing the depth distribution were chiefly food, aeration and moisture. His second paper (1922) describes the effect of farm manure on arable land at Rothamsted. He observed that the application of the farmyard manure increased the invertebrate population, but that the latter were predominantly saprophagous and not injurious to growing crops. He studied the depth of soil fauna also and concluded that the greatest number of insects and other invertebrates was confined to the upper 3 in. of the soil, though some species penetrated to a greater depth. He also attempted an estimate of nitrogen contained in the bodies of the soil fauna and found that there was no likelihood of any appreciable loss of nitrogen from the soil due to migration of the winged members of the fauna. In his third paper (1927) he gives an account of the effect of artificial manures on a soil population observed a little later in the same locality. He concluded that although artificial manures had little or no effect on the soil fauna, the effect of dung in increasing the number and the number of species was considerable.

Thompson (1924) examined an area at Aberystwyth, chiefly under grass, but with some cultivated land. The qualitative and quantitative seasonal variations observed by her were correlated with the general environmental conditions. She also found that Collembola and Acarina were markedly the dominant groups, and that the maximum population occurred during winter months, owing to relative absence of drought conditions. Edwards (1929) followed with an investigation of the insect fauna of four distinct types of soil from a permanent pasture and one from an arable land, also at Aberystwyth. He noticed that the components of the fauna differed in relation to different soil types and also attempted to correlate them with environmental conditions. He also observed that the injurious insects occurred in all four pastures with some slight variations in density.

Ford (1935) made an investigation of the animal population of soil and vegetation of the ridges transversing a meadow at certain favourable times of the year, and obtained a total density of 263·8 million individuals per acre in the soil and 8·8 million in the surface vegetation. He also observed that the greatest concentration existed between 1 to 1·5 in. below surface, few organisms below 4·5 in. and none below 8 in.; that the winter months showed a rising population to December and a falling one from January to May; and that the fluctuations were confined entirely to Collembola.

Ingram (1931) carried out a survey of the sugar-cane fields in Louisiana and showed the number of soil animals and root injury to be greatest in heavy soils. The most numerous of the injurious species were a Symphylid, *Hanseniella unguiculata*, springtails, *Lepidocyrtus violentus* and *Onychiurus armatus*, a bristle-tail, *Japyx* sp., and a snail, *Zonitoides arboreus*, their average population amounting to 10·5 million per acre. He also determined the length of time required for these soil animals to reach normal population following what he calls "extermination by flooding" and remarked: "It appears that if injurious soil animals were destroyed, benefit would be derived the year following, but the second year the soil animal population would have reached normal numbers again."

Frenzel (1936) made a comparative study of the soil fauna of some different habitats situated at elevations varying from 110 to 2000 m. in Germany and concluded that soil moisture depending upon soil structure was most important in influencing the population. He also pointed out the ecological plasticity of some of the soil organisms. In all he recorded 422 species from these habitats, with a minimum of 68 and maximum of 203 species per habitat. Peak period of the soil population in his observations occurred during October and again in early spring, and the minimum population in midwinter and midsummer.

The study of the soil fauna, as the above brief account will show, had so far been confined to the analysis of their density in relation to the environmental factors, and no qualitative data on recolonization had ever been collected.

3. Lay-out of the experiment

Allotment area

The Rothamsted Experimental Station at Harpenden is situated 25 miles north of London, at an elevation of about 400 ft. above sea-level. A small piece of land on the allotments situated in the neighbourhood of the Insectary was selected. This was bounded by a hawthorn (*Crataegus oxyacantha*) hedge about 10 ft. high on the north, by the site of a bonfire on the east and by vegetable gardens on the south and west. As the land had been uncultivated for a period of two years, it had developed a thick cover of vegetation. The latter was cleared by cultivating the entire area to a depth of 1 ft. at the end of November 1935. No further steps were taken for a month, in order to enable the soil to regain its normal activities.

Twelve plots, each 9 ft. square, were next marked out in two equal sets. One set (series A) was kept unenclosed and a margin of at least 1 ft. allowed between individual plots. Each plot in the second set (series B) was enclosed by iron sheets fixed 1 ft. below the ground and extending 6 in. above the surface. Pl. 7 shows the lay-out of the experiment at the time of first sterilization. Each set was made up of two rows each with three plots in a line. One control was allowed for every two treated plots, so that ultimately there were two sterilized

plots together with one control in each row. The selection of the plots was arrived at by a random method. The entire design of the experiment is shown in Fig. 1. The arrangement of the plots may be summarized as follows:

Series A, Unenclosed
- Sterilization I (February)
  - Plot A 01 — Control
  - Plots A 1 and A 2 — Sterilized
- Sterilization II (May)
  - Plot A 02 — Control
  - Plots A 3 and A 4 — Sterilized

Series B, Enclosed
- Sterilization I (February)
  - Plot B 01 — Control
  - Plots B 1 and B 2 — Sterilized
- Sterilization II (May)
  - Plot B 02 — Control
  - Plots B 3 and B 4 — Sterilized

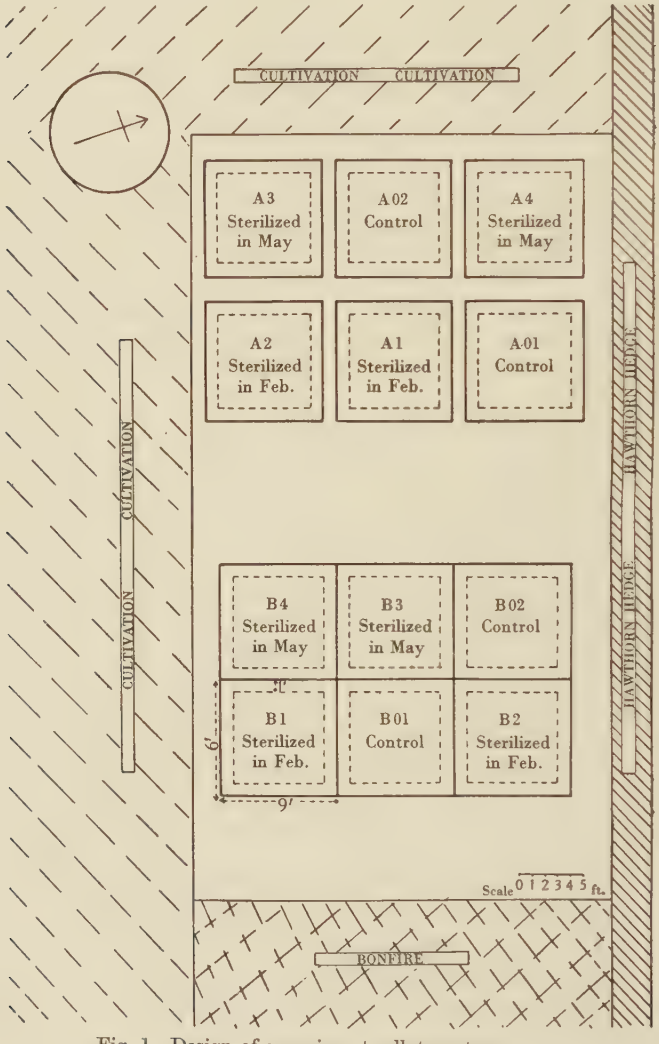
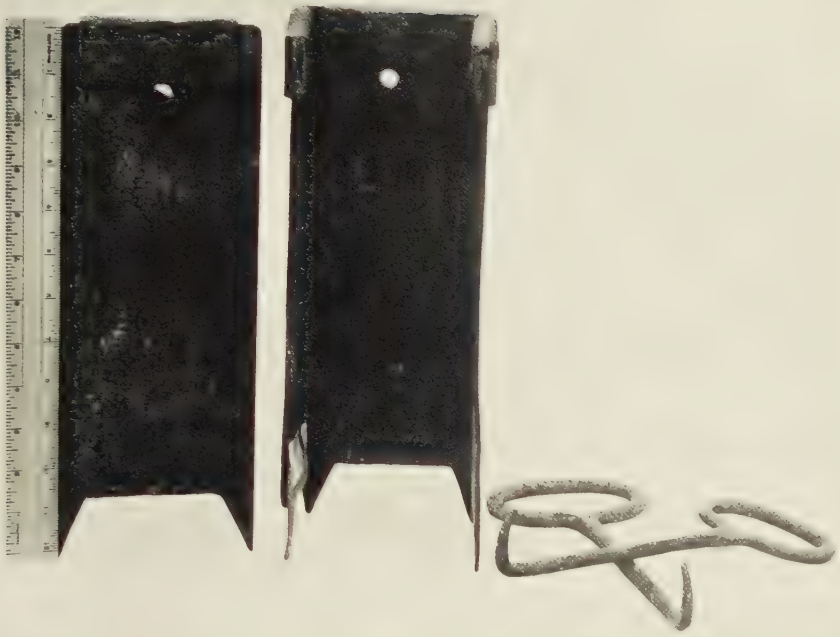
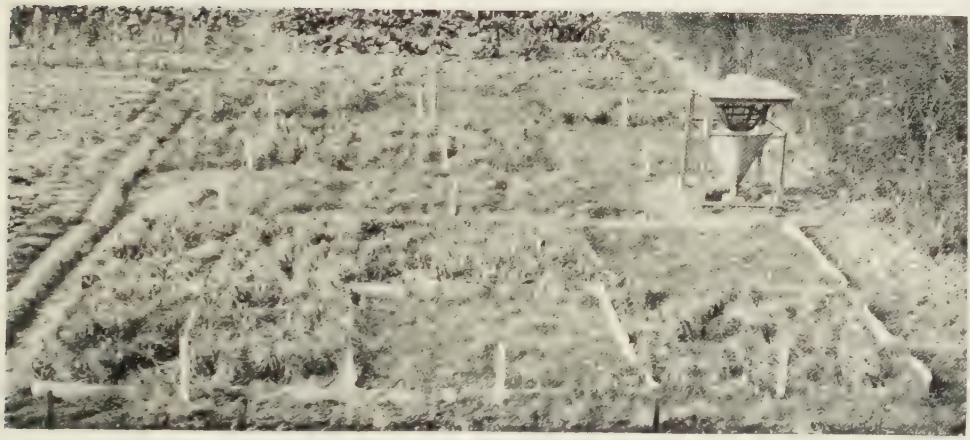


Fig. 1. Design of experiment, allotment area.

(*c*)



(*b*)



(*a*)

With the exception of the controls, the soil of all the plots was sterilized by removing it to an oven and baking it to 212° F.; the experiment was divided into two parts as explained later. Observations on all the control plots were undertaken from January 1936 and on the treated plots immediately after they were sterilized. A margin of 1 ft. was allowed inside the plots so that the actual examination of the soil fauna was made on 7×7 sq. ft.

In addition to the above, observations were also carried out on the arable as well as on the permanent pasture for purpose of comparison. These results are not included in the present paper.

4. Soil analysis

The soil of Rothamsted fields is sticky clay with a considerable amount of flints in it, overlying chalk. Mechanical analysis of all the different types of soil examined was done by the Physics Department at Rothamsted Experimental Station to whom I am indebted.

	Allotment area	
	Unenclosed %	Enclosed %
Coarse sand	11·6	10·6
Fine sand	35·5	36·5
Silt	20·0	21·5
Clay	17·5	17·5
Carbonates	—	—
Air dry moisture	3·1	2·9
Loss by solution	1·2	1·0
Loss by ignition	9·9	9·8

5. Survey of the flora

A floral survey was carried out before disturbing the soil of the allotment area. One square foot of the ground was taken at random and all the plants counted. A number of such observations were made and the density of the vegetation observed. I am grateful to Dr Winifred E. Brenchley, Rothamsted Experimental Station, who very kindly identified these plants for me.

Name of plant	Density %
1. *Poa annua* L.	41·3
2. *Galium Aparine* L.	29·4
3. *Senecio vulgaris* L.	11·4
4. *Ranunculus repens* L.	7·3
5. *Sonchus oleraceus* L.	2·9
6. *Plantago lanceolata* L.	1·3
7. Others: *Medicago lupulina* L., *Anagallis arvensis* L., *Papaver Rhoeas* L., *Daucus Carota* L., *Carum Petroselinum* B & H.F., *Sonchus* sp., *Capsella Bursa-pastoris* Moen., *Lamium album* L., and *Veronica Buxbaumii* Ten.	4·4

Throughout spring and summer weeds continued to grow in close vicinity of the plots and were removed as frequently as possible to avoid their interference with the experiment. Some stray specimens of *Euphorbia*

Helioscopia L., *Veronica Buxbaumii*, *Senecio vulgaris* and *Capsella Bursa-pastoris* were at times observed in the sterilized plots and removed. Weeding of the control plots was carried out a number of times, but the following survived in small numbers: *Matricaria inodora* L., *Anagallis arvensis*, *Convolvulus arvensis* L., *Medicago lupulina*, *Lapsana communis* L., *Lamium purpureum* L., *Euphorbia Helioscopia*, *Veronica Buxbaumii*, *Capsella Bursa-pastoris*, *Sonchus oleraceus* L., *Papaver Rhoeas* and *Plantago lanceolata*.

6. Sterilization of experimental plots

Sterilization of the soil is carried out in two ways: (*a*) by use of chemicals, (*b*) by application of heat.

(*a*) *Use of chemicals*

Chemicals are mostly employed in moderate doses for the partial sterilization of soil or for the eradication of a particular type of harmful soil organism, but in the present case complete extinction of all kinds of macro-organisms was intended and, therefore, the treatment had to be more drastic. A number of chemicals were considered: cresylic acid, carbon bisulphide, potassium cyanide, ethylene oxide, etc.; but as it was necessary that the chemical selected should possess quick toxic effect on the soil organisms and leave no residue behind, carbon bisulphide was preferred. Preliminary observations were carried out in four small plots (1×1 yard) enclosed by means of iron sheets to a depth of 1 ft., one of them having been set aside as control and the remaining three subjected to various treatments (Pl. 7*a*). Varying doses of the fumigant were tried. The plot receiving 2, 4 and 8 oz. per sq. ft. in the first treatment was given another dose of 14, 12 and 8 oz. respectively in the second. The percentage of destruction in the case of heavy doses amounted only to 95. The toxic effect was weak in action on account of the excessive soil moisture resulting from the continuous wet weather slowing down the diffusion of the carbon bisulphide. Use of still higher doses, besides being uncertain in effect, was very expensive, and this method of sterilization had to be abandoned in favour of a more satisfactory one.

(*b*) *Application of heat*

Different methods of applying heat to the soil for sterilization purposes are in vogue in England. The original idea was to sterilize the soil *in situ* so as to disturb its texture as little as possible, but the enquiries conducted for this purpose soon revealed the impractibility of the idea owing to heavy expenses involved in erecting the elaborate outfit necessary for the operation.

Baking, which is regarded as equally effective (Bewley, 1929), was resorted to. Messrs H. B. Randell, Ox Lane Nurseries, Harpenden, who possessed a "Vulcano" sterilizer (Holmes Patent No. 2057), were entrusted with the task,

and the treatment of the plots was carried out by them in a most satisfactory manner. The soil of the experimental plots was dug to a depth of 1 ft. and carted to the nursery. The temperature of the kiln was raised gradually to 212° F. and maintained for 6 hr. After treatment the soil was carted back to its respective plots. The different treatments were carried out as given below:

Sterilization 1

Plots A 1 and A 2 Unenclosed } Sterilized between 14 Feb. and 2 March
Plots B 1 and B 2 Enclosed } 1936

Sterilization 2

Plots A 3 and A 4 Unenclosed } Sterilized between 6 and 28 May 1936
Plots B 3 and B 4 Enclosed }

Before disturbing the soil for sterilization, samples were taken in order to ascertain the soil population, and the same process was repeated after it was brought back and packed into its proper position. In no instance was any living organism discovered in the baked soil, so that the recolonization of the treated plots actually started from a stage of completely eradicated macro-organic life down to a depth of 12 in.

Subsequent treatments of plots

A sample of the sterilized soil was sent for chemical analysis, and it was seen that the mineral nitrogen had considerably increased, as had been anticipated (Table 1). The chemical analysis was done by the Chemical Department of Rothamsted Experimental Station, Harpenden, to the members of which I am grateful.

Table 1. *Increase of mineral nitrogen in the sterilized plots. Mineral nitrogen mg./g.*

Plot	Before sterilization (*a*)	After sterilization (*b*)	Difference (*b* − *a*)
Sterilization 1, unenclosed plots	12·1	95	+82·9
Sterilization 1, enclosed plots	8·6	90·6	+82
Sterilization 2, unenclosed plots	13·5	62·1	+48·6
Sterilization 2, enclosed plots	11·2	73·0	+61·8

The vast increase of mineral nitrogen in the sterilized plots was due mainly to the breakdown of the organic matter forming ammonia. The sterilization had the effect of destroying the nitrifying organisms, the ammonia therefore remaining as such. In order to restore the phosphorus-nitrogen ratio, a dressing of superphosphate was given to each plot, including the controls, at the rate of 1·1 oz. per sq. yard, immediately after sterilization.

To provide some food to the recolonizating organisms, it was deemed necessary to grow some kind of crop on the plots. Various food plants will support different faunas, and after some consideration a lawn grass-seed mixture, in which rye grass (*Lolium perenne*) predominated, was selected and

raked in at the rate of 1·2 oz. per sq. yard. Germination started after about 3 weeks. The growth was very vigorous in the sterilized plots, and since it soon began interfering with the sampling process, the grass had to be mowed at regular intervals. Four such mowings were done in the sterilized plots, whereas one alone sufficed on the controls.

The grass on the sterilized plots was thicker in texture, of healthier appearance and much darker in colour than that of the controls. Pl. 7(*b*) shows the plots at the end of the observations. The difference in growth is perceptible even after a lapse of one year. The profuse growth was evidently the outcome of sterilization and it had a marked effect on the rate of recolonization of the soil organisms.

7. Technique

The Ladell apparatus (1936) was employed throughout the investigation, after it had been subjected to certain tests. The principle involved in the apparatus is flotation in a dense stratum aided by stirring the soil and bubbling a fine stream of air from below. Magnesium sulphate solution with a specific gravity of 1·11 was used. This method, besides being efficient and accurate, possesses many advantages over the previous ones, the chief being rapidity, non-toxicity and cleanliness.

(*a*) *Sampling*

One sample from the control and one from the corresponding sterilized plots of each of the unenclosed and enclosed areas were examined during each week. With this plan it was possible to examine each control twice, and the sterilized once in 4 weeks (for ease of description termed "month").

One sample could be examined in a day except during the peak period when it took a little longer. In such instances, the debris was preserved in alcohol and examined during leisure hours. During the period of the entire investigation from November 1935 to March 1937, a total of 214 samples was examined, excluding 86 which were taken from the arable and pasture lands and from other places for miscellaneous observations.

This sampling was made possible by the speed and efficiency of the Ladell's apparatus. No such previous investigations were ever extended to such a large number of samples, as will be seen from the following comparison:

Table 2. *Comparison of soil samples examined in present and past investigations*

Reference	Locality	Size of sample in.	No. of samples examined
Morris (1920)	Cheshire	10 × 10 × 24	29
Morris (1922)	Rothamsted	9 × 9 × 9	46
Morris (1927)	Rothamsted	9 × 9 × 9	45
Thompson (1924)	Aberystwyth	9 × 9 × 9	34
Edwards (1929)	Aberystwyth	9 × 9 × 9	20
Ford (1935)	Oxford	3 × 3 × 9	28
Present investigations	Rothamsted	3 × 4 × 9	300

The soil samples were taken by means of a specially designed tool (Pl. 7*c*). It was made up of iron plate 3 mm. in thickness bent to form three sides of an open rectangular chamber measuring 3×4 in. at the top and 12 in. deep. The open sides of the chamber were covered separately by iron plate of corresponding thickness and length. The lower ends of the chamber, as well as the plate, were cut out to form strong projecting teeth $1\frac{1}{4}$ in. in length and sharpened for rapid penetration into the soil. An iron plate $1\frac{1}{4}$ in. wide was fastened at the top of the chamber and the plate, with a hole below on each side for withdrawing the tool by means of iron hooks from the soil. The sampler measured 9 in. from the holes to the base of the teeth, so that when driven completely into the soil it cut a block of $3 \times 4 \times 9$ in. This was the size of the sample used throughout the experiment.

The exact position of the sample was determined by randomization. The spot was cleared of the vegetation by cutting it with a pair of scissors very close to the surface in order to exclude all above-ground forms. The sampler was then hammered into the soil and the block pulled out. The soil was transferred to a cloth bag and brought to the laboratory for further treatment. In the majority of cases it came out in a compact form, but in some instances the lower part crumbled and was gathered by hand. Each time before leaving the plot the dimension of the hole was checked by a foot rule.

The isolation of the soil fauna was carried out in the manner described by Ladell (1936), with certain modifications.

(*b*) *Rearing*

In almost all the samples which were examined, immature forms of various types were present. The majority of them were difficult to identify and had to be bred for further study. Their breeding was rendered difficult on account of the scanty numbers in which many of them occurred. As the investigation progressed their variety increased and the rearing, therefore, became more and more important. In all, 30 species of Diptera, 19 of parasitic Hymenoptera, one of Lepidoptera, and one of Orthoptera were bred from either the larval or the pupal stage to the adult. In addition, eggs were also recovered every now and again and had to be incubated for accurate information. Eggs of *Campodea* (Thysanura); *Forficula auricularia* L. (Dermaptera); *Harpalus*, *Amara*, *Tachyporus*, *Quedius*, *Philonthus*, *Staphylinus*, *Lacon*, *Chaetocnema* (Coleoptera); *Acocephalus* and *Nabis* (Hemiptera); *Agrotis* and two undetermined spp. (Lepidoptera); one undetermined sp. probably *Lithobius* (Myriopoda); two undetermined spp. of Araneida (Spider); and *Arion* (Gastropoda) were thus determined.

(c) *Preservation of material*

Insects which could not be pinned or mounted properly were preserved in 70% alcohol. Special treatment was necessary for the detailed study of the following:

Collembola. Air bubbles which always adhered to the body of the Collembola interfered with counting. Handschin (1929) recommends the use of a few drops of chloroform to overcome this trouble, but it was not found satisfactory. Immersion of the tube containing the specimens in water-bath (95° F.) for a minute or so followed by gentle shaking, proved quite useful. Besides, the heat served to stretch the insects, facilitating their quick provisional determination. For more detailed study, mounts were made in Berlese fluid.

Larvae. Larvae were killed in boiling water. This process, though it slightly extended their bodies, possessed the advantage, especially in Diptera, of retaining their colour which in alcohol generally turned greyish black otherwise.

Acarina. They were cleared in Koenike's fluid for a few days before mounting.

8. Effect of the hawthorn hedge on the soil population

The hawthorn hedge (Fig. 1), which formed a barrier on the north about 3 ft. away from the experimental plots of the allotment area, might have been expected to have an influence on the density of the soil organisms in its neighbourhood. In the course of investigations it became apparent that some observations were essential to elucidate this point. The narrow strip lying between the plots and the hedge was examined at different positions in April 1936. The relationship of population of the strip and the adjoining controls at the corresponding periods is worked out below:

Soil population per sample

Narrow strip	Control	Increase
105	46	×2·3
251	169·5*	×1·5
143	68·5*	×2·1

* Mean of two observations.

The population in the strip proved 1·5–2·3 times higher than the controls. It seems likely that the breaking up of the soil in this experimental area in November 1935, prior to sterilization, compelled the subterranean forms to seek retreat under the base of the hedge where they stayed till the approach of the warm weather, hence the strip displayed higher population figures. These observations are unfortunately too few for any definite conclusion. The matter becomes more clear when we take the annual population of the controls into consideration. The average figures of the organisms per sample work out as follows:

Control plots close to the hedge:

B 02 (enclosed)	143·3
A 01 (unenclosed)	138·3

Control plots away from the hedge:

B 01 (enclosed)	105
A 02 (unenclosed)	135·8

It will be seen that excepting plot B 01 all the rest closely approximated to one another. The case of B 01 appears rather exceptional, and as it was situated away from the hedge, its low population may have been influenced by some entirely different factors, one of which is suggested below. Leaving this plot aside, it will be seen that the hedge exercised no marked influence on the plots situated in its close neighbourhood.

A comparison of the more important components in these four controls shows that the chief difference in plot B 01 was due to the low proportion of Collembola, Myriopoda and Arachnida (Table 3). On account of its extreme end position this portion of the allotment area was reported to have been less cultivated previously than the others. Under the circumstances its soil had become comparatively more compact. This phenomenon was also observed in the earlier part of the experiment when cultivation was undertaken. It is quite possible that the compactness of the soil may have resulted in the low density of its soil organisms which effected its later developments.

Table 3. *Average soil population per sample in control plots*

	Insects				Other invertebrates				
Control plots	Collembola	Immature forms	Other insects	Total	Myriopoda	Arachnida	Other invertebrates	Total	Grand total
A 01 unenclosed	78·1	17·9	3·5	99·5	22·4	11·2	5·2	38·8	138·3
A 02 unenclosed	61·8	20·9	3·5	86·2	25·4	17·8	6·4	49·6	135·8
B 01 enclosed	41·9	33	4·1	79	12·8	9·1	4·1	26	105
B 02 enclosed	70·6	20·1	8·2	98·9	24·4	14·9	5·1	44·4	143·3

9. Composition of the soil fauna

(*a*) *General comparison*

The allotment area, excepting for the breaking up of its soil in November 1935, followed by sowing of lawn grass and application of superphosphates, did not receive any other treatment and thus remained under more or less constant conditions. Since intensive study of the soil fauna was carried out here, it is thought to represent the activities of the soil organisms more or less accurately.

In England the soil fauna has always been observed to belong to the following orders. Insecta: Collembola, Thysanura, Orthoptera (Dermaptera), Thysanoptera, Hemiptera, Lepidoptera, Coleoptera, Diptera, Hymenoptera, and Psocoptera. Other invertebrates: Myriopoda, Arachnida, Isopoda, Oligochaeta, Nematoda and Gastropoda.

In addition to these, a specimen of Protura was discovered in August 1936, but unfortunately could not be identified. It has not so far been recorded in any one of the previous soil investigations, although Williams (1913) found many in turf and soil.

Immature forms (eggs, larvae and pupae) of all the insect orders except Collembola, Thysanoptera and Psocoptera, were frequently encountered in the soil samples. Next to the Collembola (44–58·7%) they formed 14·3–42·2% of the total soil fauna (Table 4).

Table 4. *Percentage composition of soil fauna*

	Collembola	Immature forms	Other insects	Total insects	Other invertebrates
Allotment area, unenclosed:					
Control	49·2	14·3	2·6	66·1	33·9
Sterilization 1	53	32·8	3·8	89·6	10·4
Sterilization 2	58·7	29·6	5·0	93·3	6·7
Allotment area, enclosed:					
Control	44	21	6·2	71·2	28·8
Sterilization 1	48·9	42·2	4·6	93·7	6·3
Sterilization 2	53·9	39·3	2·0	95·2	4·8

The highest figures of the total soil population determined by various methods and workers on different types of soil are compared in Table 5. All other estimates of the soil population, excepting that of Ford, are much below similar figures obtained during the present investigations. The population on the allotment controls varied between 61·2 to 67·6 million per acre. In one of the sterilized plots a maximum figure of 513·8 million per acre was recorded in December 1936. Ford confined his attention to a richly populated habitat (ridges of a meadow land) and carried out his observations only during those periods of the year when one would have expected the figures to be high. Under such circumstances his estimate was bound to be high, and with the present method it might have been still higher.

(*b*) *Controls*

In the calculation of the monthly means of the fauna both the controls and the two corresponding sterilized plots in the unenclosed and the enclosed areas have been considered together. The mean soil populations of the controls (Table 6) approximated to each other, viz. 67·6 million per acre in the unenclosed and 61·2 million in the enclosed. The difference of 6·4 million per acre in the enclosed control is mainly due to the abnormal behaviour of plot B 01 already discussed. The prominent constituents of the entire association were Collembola, Diptera and Coleoptera, and to some small extent Hemiptera and Hymenoptera (among insects), and Myriopoda, Arachnida and Oligochaeta (among other invertebrates). Their density (Figs. 2*a*, 3*a*) is more or less the same, except that Collembola, Coleoptera and Myriopoda in the unenclosed plots and Diptera and Hymenoptera in the enclosed ones showed slightly higher

Table 5. *Soil populations as determined by various methods*

Worker	Year	Locality	Type of soil examined	No. of samples examined	Average invertebrate population per acre in millions	Percentage of population		Remarks
						Insects	Other invertebrates	
McAtee	1907	Washington, U.S.A.	Forest floor	1	1·2	24·1	75·9	—
			Meadow land	1	13·6	80·2	19·8	About 73% were ants
Cameron	1913–14	Cheshire	Glover's meadow	11	0·8			Insects only
			Alluvial pasture field	14	1·5			—
Morris	1916–17	Cheshire	Lane field pasture	29	3·5			Insects only
Morris	1920–21	Rothamsted, Hertfordshire	Broadbalk (arable), manured dung	23	15·1	57·2	48·8	—
			Broadbalk (arable), unmanured	23	5·0	49·9	50·1	—
Thompson	1920–21	Aberystwyth, Cardiganshire	Pasture land	20	19·5	43·8	56·2	—
Edwards	1925–26	Aberystwyth	Pasture	20	27·2–44·6	48·3–69·2	51·7–32·8	—
Ford	1931–33	Oxford	Meadow (ridges)	16	263·8	92·8	7·2	See Note 1
Baweja (Ladell's apparatus)	1935–37	Rothamsted	Allotment, unenclosed, control	61	67·6	66·1	33·9	—
			Allotment, unenclosed sterilization 1	26	98·4	89·6	10·4	—
			Allotment, unenclosed sterilization 2	20	111·8	93·3	6·7	—
			Allotment, enclosed, control	61	61·2	71·2	28·8	—
			Allotment, enclosed, sterilization 1	26	109·0	93·7	6·3	See Note 2
			Allotment, enclosed, sterilization 2	20	110·2	95·2	4·8	—

Note 1. Observations were carried out in two springs and one winter, excluding the intervening summer and autumn, hence his figures are high.

Note 2. In one of these observations population went up to 513·8 million per acre.

numbers. The immature forms of the insects alone formed a density of 9·7 million per acre in the unenclosed and 13·5 million in the enclosed plots, out of which Diptera and Coleoptera constituted 70 and 22·5% in the former and 88·1 and 8·7% in the latter. The proportion of insects to other invertebrates was 2 : 1 in the first instance and 2·4 : 1 in the second.

(*c*) *Sterilized plots*

The study of the mean soil population of the sterilized plots (Table 7) shows that the principal constituents remained the same as in the controls, but the density of their population was markedly different in various groups. Immature forms of insects made up a concentration of 32·46 million per acre in these plots, in which Diptera and Coleoptera predominated as shown under:

Plot	Treatment	Population: immature forms million per acre	Percentage: immature forms	
			Diptera	Coleoptera
Unenclosed:	Sterilization 1	32·253	94·4	3·3
	Sterilization 2	33·062	94·0	4·1
Enclosed:	Sterilization 1	45·999	95·6	3·2
	Sterilization 2	43·333	95·0	3·9

During the period of 13 months' investigation after sterilization 1 and 10 months after sterilization 2, the soil population had not only regained the original figures, but had increased beyond them. This increase reckoned as a proportion of controls varied as given below. Its rate in the enclosed plots was comparatively quicker and slightly higher.

Unenclosed plots:	
Sterilization 1	1·5 times
Sterilization 2	1·7 times
Enclosed plots	
Sterilization 1	1·8 times
Sterilization 2	1·8 times

The proportion of insects and other invertebrates, which was 2 : 1 in the controls, was very much altered, having reached a maximum of nearly 20 : 1 in one of the sterilized plots. The following comparison illustrates this disturbance in detail:

		Sterilization	
	Control	1	2
Unenclosed	2 : 1	8·6 : 1	13·9 : 1
Enclosed	2·4 : 1	14·9 : 1	19·8 : 1

A further study of the relative increase of the more abundant orders in the sterilized plots (Table 8, Figs. 2*b*, *c*, 3*b*, *c*) shows that among the insects Collembola and Diptera were the foremost to return. With the exception of these two orders, and in addition Hemiptera, Coleoptera and to a lesser extent

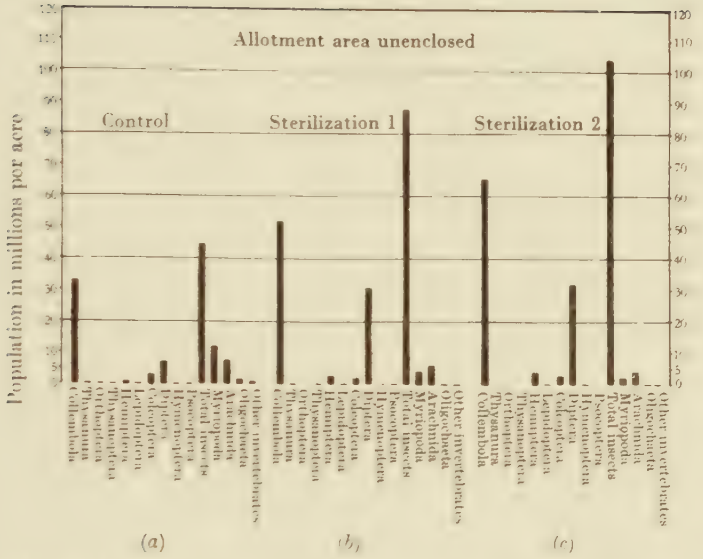


Fig. 2. Mean soil population of the allotment area, unenclosed plots. (*a*) Control. (*b*) sterilization 1. (*c*) sterilization 2.

Fig. 3. Mean soil population of the allotment area, enclosed plots. (*a*) Control, (*b*) sterilization 1, (*c*) sterilization 2.

Table 6. *Mean soil population of allotment area controls in millions per acre*

	Insecta										
Plot	Protura	Collembola	Thysanura	Orthoptera	Thysanoptera	Hemiptera	Lepidoptera	Coleoptera	Diptera	Hymenoptera	Psocoptera	Total
Unenclosed	—	33·245	0·209	0·005	0·042	0·889	0·052	3·189	6·848	0·209	0·020	44·708
Enclosed	0·005	26·920	0·157	0·052	0·105	1·202	0·031	1·725	11·918	1·255	0·183	43·553

	Other invertebrates							
Plot	Myriopoda	Arachnida	Isopoda	Oligochaeta	Nematoda	Gastropoda	Total	Grand total
Unenclosed	12·179	7·527	0·575	1·725	0·627	0·261	22·894	67·602
Enclosed	9·148	6·116	0·157	1·098	0·993	0·078	17·590	61·143

Table 7. *Mean soil population of sterilized plots*

	Insecta									
Plots	Collembola	Thysanura	Orthoptera	Thysanoptera	Hemiptera	Lepidoptera	Coleoptera	Diptera	Hymenoptera	Psocoptera	Total
Unenclosed										
Sterilization 1	52·115	0·314	—	0·02	2·614	0·157	1·986	30·789	0·084	—	88·079
Sterilization 2	65·68	-	-	—	3·947	0·052	2·587	31·886	0·157	—	104·309
Enclosed											
Sterilization 1	51·174	0·078	0·02	0·37	3·136	0·522	2·979	44·431	0·157	0·02	102·887
Sterilization 2	59·407	0·078	—	0·105	1·28	0·052	2·405	41·452	0·052	0·105	104·936

	Other invertebrates							
Plots	Myriopoda	Arachnida	Isopoda	Oligochaeta	Nematoda	Gastropoda	Total	Grand total
Unenclosed								
Sterilization 1	3·92	5·854	0·052	0·261	0·105		10·192	98·271
Sterilization 2	2·3	4·312	0·34	0·444	0·078	0·026	7·500	111·809
Enclosed								
Sterilization 1	1·829	4 6	0·261	0·105	0·037	0·037	6·869	109·756
Sterilization 2	0·784	4·286	0·13	0·078	-	-	5·278	110·214

Thysanura and Lepidoptera, none of the other invertebrates was able to reach the normal population in this period. Although Hemiptera show a considerable increase over the control and also Coleoptera to some extent, their relative density was low due to the rapid growth of Collembola and Diptera, which really predominated in the whole course of recolonization.

Table 8. *Relative increase of soil population of the sterilized plots over the control*

Plots	Sterilization	Collembola	Hemiptera	Coleoptera	Diptera	Total insects	Myriopoda	Arachnida	Other invertebrates	Total population
Unenclosed	1	1·6	2·9	0·6	4·5	2·0	0·3	0·8	0·4	1·5
	2	2·0	4·4	0·8	4·7	2·3	0·2	0·6	0·3	1·7
Enclosed	1	1·9	2·6	1·7	3·7	2·3	0·2	0·8	0·4	1·8
	2	2·2	1·0	1·4	3·5	2·4	0·1	0·7	0·3	1·8

Considering the immature forms of insects, it is to be seen that their increase over the controls was 3·3 and 3·4 times in the unenclosed, sterilizations 1 and 2, and 3·4 and 3·2 times in the enclosed, sterilizations 1 and 2. In this series 3·1 and 3·2 times in the former and 3·2 and 3·0 times in the latter were constituted by Diptera alone.

It seems clear that the sterilized soil encouraged the increase of soil organisms, particularly insects, some of which, namely Collembola and Diptera, multiplied very rapidly, not only upsetting the normal ratio but taking the population to a very high level of density.

10. Normal seasonal changes

In a study of this kind where many organisms belonging to different orders with a multitude of individual and collective variations are involved, it is impossible to consider each one of them separately. Only those which were regularly present during the investigation and formed a high proportion of the population have been selected for discussion. Insects formed a major proportion of the soil fauna, this being chiefly composed of Collembola and the immature forms, which were in turn mostly Diptera. Therefore attention is directed to these groups. Mean monthly population figures per sample are worked out in Tables 9–14. Dividing the figures on these tables by 2 will convert them into approximate population of millions per acre (Baweja, 1937).

(*a*) *Unenclosed controls*

The population curve (Fig. 4*a*) shows that the total population of the unenclosed controls was considerably lower during the winter. With the approach of warm weather it began to rise gradually and continued to do so till the middle of September, after which there was a sudden increase in some of the soil organisms, a peak being reached by about the middle of November.

Table 9. *Mean monthly soil population per sample. Allotment area, unenclosed, controls*

Mean date of monthly sampling period	Insecta												Other invertebrates							
	Collembola	Thysanura	Orthoptera	Thysanoptera	Hemiptera	Lepidoptera	Coleoptera	Diptera	Hymenoptera	Psocoptera	Eggs, larvae and pupae	Total	Myriopoda	Arachnida	Isopoda	Oligochaeta	Nematoda	Gastropoda	Total	Grand total
1936																				
1 Feb.	28·5	0·3	—	0·1	—	—	0·4	—	—	0·3	13·6	43·2	5·3	12·1	0·7	7·7	0·3	0·3	26·4	69·6
29 Feb.	14·5	0·5	—	0·5	—	—	1·5	—	—	—	13	30	16	9	3·5	3	—	0·5	32	62
28 Mar.	27·7	—	—	—	—	—	1·7	—	0·3	—	6	35·7	29·5	10·7	2·5	1·5	0·3	0·5	45	80·7
25 Apr.	13·7	0·8	—	0·2	—	—	3·6	—	—	—	16·2	34·5	26·6	14·5	3·1	1·8	0·8	0·8	47·6	82·1
23 May	20	0·3	—	0·3	—	—	1·4	—	—	—	4·3	26·3	16·7	10·7	1·6	13	2	—	44	70·3
20 June	33·4	0·1	—	—	0·3	—	2·6	—	0·1	—	9·5	46	32·6	9	0·5	0·8	0·9	—	43·8	89·8
18 July	33·1	1·1	—	—	0·1	—	2·4	0·3	2·4	—	14·1	53·5	33·6	11	0·5	1·3	0·5	—	46·9	100·4
15 Aug.	46	0·1	—	—	1·8	—	2·8	—	0·5	—	17·8	69	25·6	11·4	1	3·7	1·4	—	43·1	112·1
12 Sept.	45·4	0·5	—	—	0·5	—	0·6	—	0·3	—	14·5	61·8	20	8·4	0·5	1·7	0·9	0·5	32	93·8
10 Oct.	135·9	0·6	—	—	1·8	—	1·1	—	0·2	—	30·4	170	33·4	11·8	0·8	2·1	2·9	—	51	221
7 Nov.	206·5	0·4	—		0·6	-	2·5	0·6	0·4	0·4	27·1	238·5	26·5	24·2	0·6	4·3	1·6	0·4	57·6	296·1
5 Dec.	95·4	0·3	0·2	—	1·1	—	1·1	—	—	—	29·4	127·5	20·4	14·9	—	1·5	2·8	2	41·6	169·1
1937																				
2 Jan.	107	0·2			0·8		2·1		0·4	-	34·8	145·3	18·3	24·5	0·5	1·9	0·4	0·5	46·1	191·4
30 Jan.	No observations made																			
27 Feb.	83·5	—	—	—	—	—	2·5	—	0·5	—	29	115·5	21·5	29·5	—	2	2	1·5	56·5	172

Table 10. *Mean monthly soil population per sample. Allotment area, unenclosed plots -sterilization* 1

Mean date of monthly sampling period	Insecta												Other invertebrates							
	Collembola	Thysanura	Orthoptera	Thysanoptera	Hemiptera	Lepidoptera	Coleoptera	Diptera	Hymenoptera	Psocoptera	Eggs, larvae and pupae	Total	Myriopoda	Arachnida	Isopoda	Oligochaeta	Nematoda	Gastropoda	Total	Grand total
1936																				
29 Feb.	—	—	—	—	—	—	—	—	—	—	—	0	—	—	—	[illegible]	[illegible]	[illegible]	0	0
28 Mar.	2·5	1·5	—	—	—	—	—	—	0·5	—	1·5	6·0	5	1·0	—	[illegible]	[illegible]	[illegible]	6·0	12
25 Apr.	4·5	—	—	—	—	—	1·5	—	—	—	4·5	10·5	1	[illegible]	—	[illegible]	[illegible]	[illegible]	1	11·5
23 May	14·5	—	—	—	—	—	—	—	—	—	7	21·5	6·5	1	—	[illegible]	—	[illegible]	7·5	29
20 June	11	—	—	—	1	—	1·5	0·5	—	—	6	20	7·5	—	[illegible]	—	[illegible]	[illegible]	7·5	27·5
18 July	42·5	—	—	—	0·5	—	3·5	0·5	—	—	28	75	9·5	5·5	0·5	0·5	—	—	16	91
15 Aug.	46·5	—	—	—	1·5	—	0·5	0·5	0·5	—	17·5	67	2	2·5	0·5	—	—	—	5	72
12 Sept.	56·5	—	—	—	2	—	1	—	1	—	19·5	80	8·5	8·5	0·5	2·5	1	—	21	101
10 Oct.	167·5	2	—	—	5·5	—	4	1	—	1	138·5	319·5	21·5	15	—	0·5	0·5	—	37·5	357
7 Nov.	175·5	—	—	—	13	—	2	1	—	—	166·5	358	5·5	27	—	1	0·5	—	34	392
5 Dec.	231·5	0·5	—	—	3·5	—	2	0·5	—	0·5	157·5	396	9·5	27	—	0·5	—	—	37	433
1937																				
2 Jan.	262	1	—	0·5	20·5	—	5	2·5	—	0·5	150	442	11	38·5	—	1·5	—	—	51	493
30 Jan.	No observations made																			
27 Feb.	281·5	—	—	—	7·5	—	2·5	1	—	—	105·5	398	10	19	—	0·5	0·5	—	30	428

Table 11. *Mean monthly soil population per sample. Allotment area, unenclosed plots—sterilization 2*

Mean date of monthly sampling period	Insecta												Other invertebrates							
	Collembola	Thysanura	Orthoptera	Thysanoptera	Hemiptera	Lepidoptera	Coleoptera	Diptera	Hymenoptera	Psocoptera	Eggs, larvae and pupae	Total	Myriopoda	Arachnida	Isopoda	Oligochaeta	Nematoda	Gastropoda	Total	Grand total
1936																				
23 May	—	—	—	—	—	—	—	—	—	—	—	0	—	—	—	—	—	—	0	0
20 June	1						2				3·5	6·5	1·0	2·0					3·0	9·5
18 July	5	—	—	—	1·5	—	2·5	—	—	—	13·5	22·5	—	4·0	—	—	—	—	4·0	26·5
15 Aug.	35	—	—	—	8	—	1·5	0·5	—	—	28·5	73·5	3	2	0·5	1·5	—	—	7	80·5
12 Sept.	43·5	—	—	—	7	—	1	0·5	1	—	29·5	82·5	3·5	2	—	1·5	—	—	7	89·5
10 Oct.	59·5	—	—	—	2·5	—	2	—	—	—	99·5	163·5	7·5	3	1·5	0·5	0·5	—	13	176·5
7 Nov.	179	—	—	—	11·5	—	1	5·5	—	—	79·5	276·5	11·5	6·5	0·5	1	—	—	19·5	296
5 Dec.	227	—	—	—	6·5	—	5	5·5	—	—	95·5	339·5	10	23	—	1	—	0·5	34·5	374
1937																				
2 Jan.	298·5	—	—	—	2·5	—	7	1	0·5	—	129·5	439	2·5	25·5	1·0	0·5	—	—	29·5	468·5
30 Jan.	No observations made																			
27 Feb.	408	—	—	—	26·5	—	1·5	2·5	—	—	153·5	592	5	14·5	3	2·5	1	—	26	618

Table 12. *Mean monthly soil population per sample. Allotment area, enclosed controls*

Mean date of monthly sampling period	Insecta													Other invertebrates							
	Protura	Collembola	Thysanura	Orthoptera	Thysanoptera	Hemiptera	Lepidoptera	Coleoptera	Diptera	Hymenoptera	Psocoptera	Eggs, larvae and pupae	Total	Myriopoda	Arachnida	Isopoda	Oligochaeta	Nematoda	Gastropoda	Total	Grand total
1936																					
1 Feb.	—	24·3	—	—	0·3	—	—	0·2	—	0·2	0·2	8·0	33·2	2·2	9·3	0·2	2·6	—	0·3	14·6	47·8
29 Feb.	—	15	—	—	—	—	—	1	—	—	—	15	31	4	7	1	1·5	0·5	—	14·0	45
28 Mar.	—	26·2	0·7	—	—	0·7		0·3	—	16·3	—	30	74·2	17·2	8·6	—	0·5	1	0·2	27·5	101·7
25 April	—	27·1	0·2	—	—	—		1·2	—	0·2	—	20·8	49·5	17·8	31·7	0·3	4	3·3	0·7	57·8	107·3
23 May	—	23·6	0·3	0·7				1·0	—	0·7	—	11·7	38	16·3	5·7	0·3	7·7	3	0·3	33·3	71·3
20 June	—	24	—	—	0·3	0·5		0·5	0·4	3·6	0·4	8·1	37·8	23·6	6·1	0·6	3	1·5	—	34·8	72·6
18 July	0·1	31·4	0·1	—		4		1·9	—	3·3	0·2	13·5	54·5	20·5	7·7	0·4	0·9	1	—	30·5	85
15 Aug.	—	41·9	0·6	—		2·1		0·9	—	3·1	—	12·9	61·5	15·4	5·2	0·5	1	1·4	—	23·5	85
12 Sept.	—	38·4	0·3	—	0·5	2·1		1·6	—	0·6	—	18	61·5	12	8·1	0·3	2·6	4·4	—	27·4	88·9
10 Oct.	—	69·2	—	0·2	0·5	—		0·3	0·2	0·8	1	43	115·2	24	8·8	—	—	2·5	—	35·3	150·5
7 Nov.	—	145·6	1·1	—	1·2	2·1	—	2·4	0·3	0·9	2·1	55	210·7	34	37·6	0·3	1·5	4·8	0·1	78·3	289
5 Dec.	—	139	0·8	—	0·4	2·8	—	1·2	—	0·5	0·2	44·1	189	23·6	11·9	0·2	1·9	0·4	—	38	227
1937																					
2 Jan.	—	88·6	0·2	—	0·2	1·4		0·5	—	—	0·3	46·8	138	22·4	10·8	—	2·2	2·2	0·5	38·1	176·1
30 Jan.	No observations made																				
27 Feb.	—	26·5	—	—	—	6	—	2	—	4	0·5	34	73	11·5	5·5	—	0·5	0·5	—	18	91

Table 13. *Mean monthly soil population per sample. Allotment area, enclosed plots—sterilization* 1

Mean date of monthly sampling period	Insecta												Other invertebrates							
	Collembola	Thysanura	Orthoptera	Thysanoptera	Hemiptera	Lepidoptera	Coleoptera	Diptera	Hymenoptera	Psocoptera	Eggs, larvae and pupae	Total	Myriopoda	Arachnida	Isopoda	Oligochaeta	Nematoda	Gastropoda	Total	Grand total
1936																				
29 Feb.	—	—	—	—	—	—	—	—	—	—	—	0	—	—	—	—	—	—	0	0
28 Mar.	—	—	—	—	—	—	2·5	—	2	—	0·5	5	2	—	—	—	—	—	2·5	7·5
25 Apr.	12·5	—	0·5	—	—	—	1	—	—	—	1·5	15·5	1	2·5	—	—	—	—	3·5	19
23 May	6	—	—	—	—	—	—	—	—	—	3·5	9·5	1	2	—	—	—	—	3	12·5
20 June	12·5	—	—	—	0·5	—	—	—	—	—	5	18	1	0·5	—	—	0·5	—	2	20
18 July	29·5	—	—	—	1·5	—	5·5	—	0·5	—	43	80	1	6	1	—	—	—	8	88
15 Aug.	73·5	0·5	—	—	3·5	—	1	0·5	0·5	—	25	104·5	3	8·5	1	—	—	—	12·5	117
12 Sept.	70	—	—	—	21·5	—	3	—	—	—	28	122·5	2·5	10·5	—	0·5	—	—	13·5	136
10 Oct.	77	0·5	—	—	2	—	—	—	—	—	83·5	163	8·5	10	0·5	—	—	—	19	182
7 Nov.	240	0·5	—	1	1	—	6·5	6	0·5	—	117	372·5	4	23	2	1	—	1	31	403·5
5 Dec.	313·5	0·5	—	—	1	—	8·5	4·5	—	0·5	231	559·5	5·5	22	1	—	0·5	—	29	588·5
1937																				
2 Jan.	301·5	—	—	—	32·5	—	7	—	—	—	347	688	8	17·5	0·5	0·5	—	—	26·5	714·5
30 Jan.	No observations made																			
27 Feb.	136	—	—	—	3·5	—	2·5	0·5	0·5	—	258·5	401·5	8	12·5	0·5	0·5	—	—	21·5	423

Table 14. *Mean monthly soil population per sample. Allotment area, enclosed plots—sterilization 2*

Mean date of monthly sampling period	Insecta												Other invertebrates							
	Collembola	Thysanura	Orthoptera	Thysanoptera	Hemiptera	Lepidoptera	Coleoptera	Diptera	Hymenoptera	Psocoptera	Eggs, larvae and pupae	Total	Myriopoda	Arachnida	Isopoda	Oligochaeta	Nematoda	Gastropoda	Total	Grand total
1936																				
23 May	—	—	—	—	—	—	—	—	—	—	—	0	—	—	—	—	—	—	0	0
20 June	0·5	—	—	—	—	—	—	—	—	—	3	3·5	—	—	—	—	—	—	—	3·5
18 July	9	—	—	—	1	—	1	1	—	—	27	39	1·5	0·5	—	—	—	—	2	41
15 Aug.	31·5	—	—	—	3·5	—	1	0·5	—	—	32	68·5	—	3·5	0·5	—	—	—	4·0	72·5
12 Sept.	40	—	—	—	7	—	1	0·5	—	—	15·5	64	2·5	5	0·5	—	—	—	8	72
10 Oct.	61·5	—	—	0·5	2	—	1·5	0·5	—	—	*98	164	—	4·5	—	—	—	—	4·5	168·5
7 Nov.	273·5	—	—	0·5	0·5	—	1	1	—	0·5	124·5	401·5	1	26	1	1	—	—	29	430·5
5 Dec.	175·5	1·5	—	—	1	—	1·5	0·5	—	0·5	120	300·5	5	12·5	—	—	—	—	17·5	318
1937																				
2 Jan.	241	—	—	—	—	—	3·5	0·5	0·5	1	221	467·5	2·5	24·5	—	—	—	—	27	494·5
30 Jan.	No observations made																			
27 Feb.	304	—	—	1	1·5	—	3	1	0·5	—	188	499	2·5	5·5	0·5	0·5	—	—	9	508

* Discovered colony of 454 *Trichocera* (?) larvae, not included in totals.

It was soon after followed by an equally rapid fall which tended to bring the population back to its winter level.

The insect population curve shows that insects formed a high proportion of the total population—62 % at the beginning of the observations in February 1936. By about the end of April their number had gone down, and the percentage was 42. After this they started increasing and during the peak period formed 80 %. This peak occurred about the second week of November, and at the end of the observations the proportion had dropped to 67 % of the total

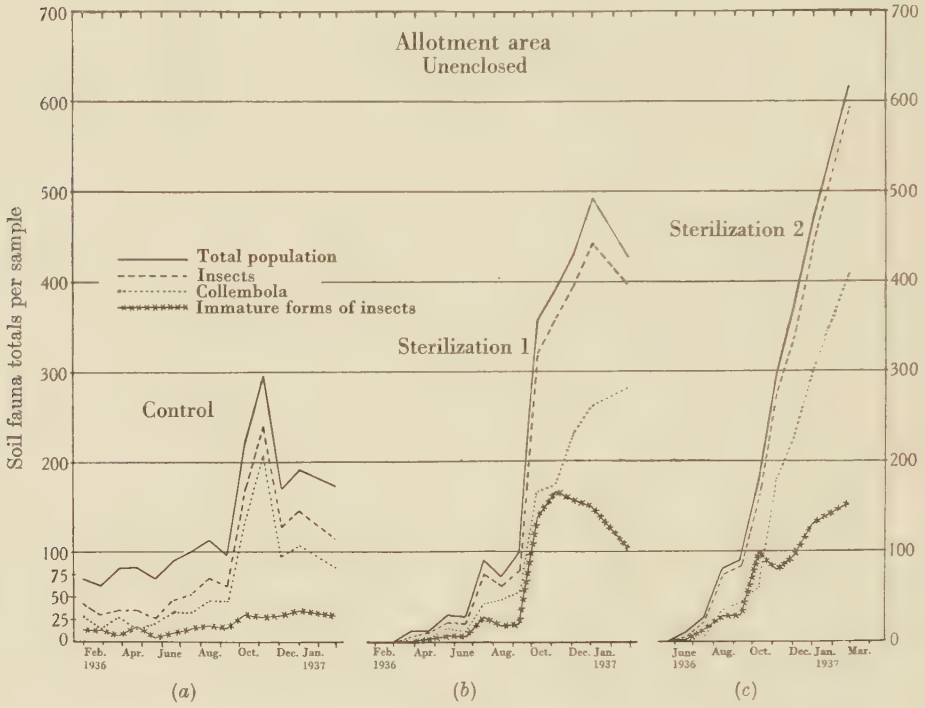


Fig. 4. Monthly variations of the soil fauna (mean numbers per sample). Allotment area, unenclosed plots. (*a*) Control, (*b*) sterilization 1, (*c*) sterilization 2.

population. Collembola formed 41 % at the beginning, and the immature forms (mostly Diptera) 20 %. Collembola then, after a slight rise, fell down to 17 % at the end of April, and growing steadily afterwards formed 70 % of the population during the peak period, falling down to 48 % at the end; while the immature forms fell down to 6 % during the end of May and then gradually increasing came to form 9 % during the peak period and 17 % at the end. The immature forms had in fact increased during summer and autumn, but as their number could not keep pace with the sudden and profuse growth of Collembola their percentage fell.

It will be shown that the weather at the end of April was unfavourable for soil insects in general and Collembola in particular, while the immature forms seemed to suffer a month later, i.e. at the end of May.

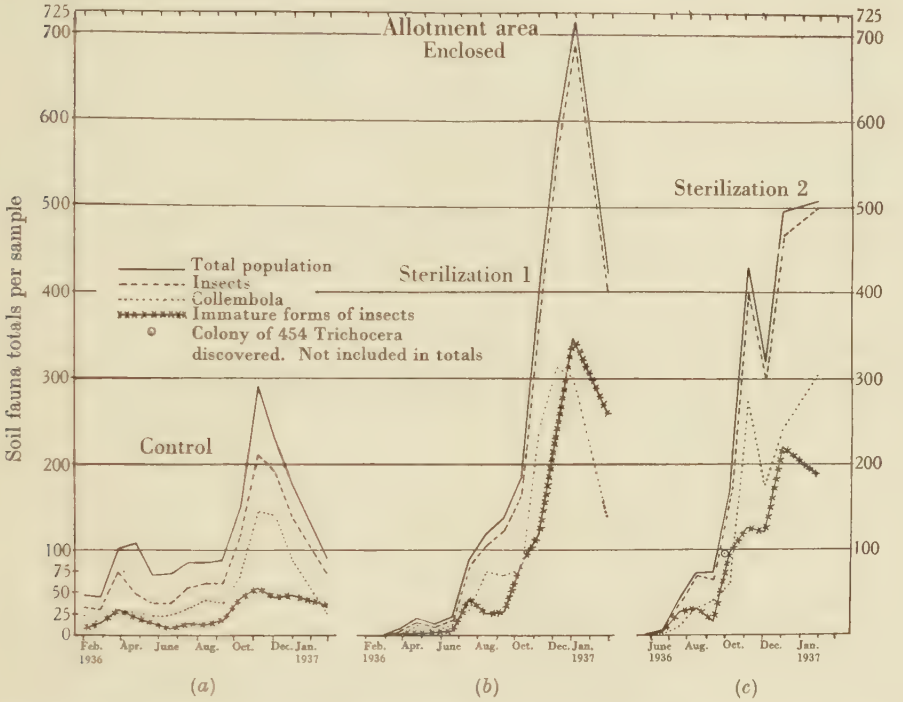


Fig. 5. Monthly variations of the soil fauna (mean numbers per sample). Allotment area, enclosed plots. (*a*) Control, (*b*) sterilization 1, (*c*) sterilization 2.

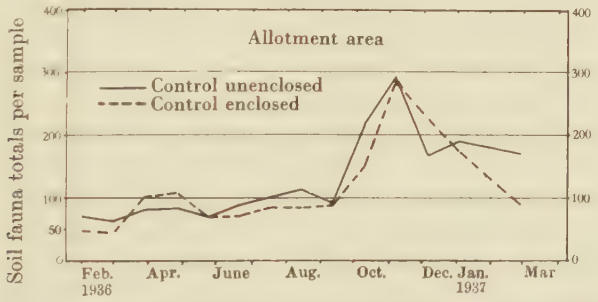


Fig. 6. Comparison of total soil fauna of unenclosed and enclosed controls, allotment area.

(*b*) *Enclosed controls*

The total population of the enclosed controls (Figs. 5*a*, 6) followed more or less the same course as the unenclosed ones except a small rise during March–May. Both (Fig. 6) developed their peaks at the same time, i.e. middle of

November. Insects formed 70% of the total population at the beginning and, as in the case of unenclosed, came down to 46% by the end of April, started rising again and formed 73% during the peak period, and 80% at the end. Collembola started with 51%, fell down to 25% by the end of April, rose to 50% during the peak and ended at 29%. The immature forms started with 17%, and after a slight rise to 19% towards the end of April fell to 15% in the middle of August, increased to 19% during the peak and to 37% at the conclusion of the observations.

It will be seen that the insects in these plots, as well as on the unenclosed ones, showed a decline towards the end of April, Collembola being affected particularly, while the immature forms suffered a little later.

A consideration of these plots shows that the soil population is subject to variations during different periods of the year. The population is at its low level during the winter. With the approach of the warm weather there is a definite tendency to rise and this is maintained throughout the summer. A sudden increase during autumn or early winter, due mostly to the marked increase of Collembola, results in the peak period. The latter is short in duration and is soon followed by an equally rapid fall which tends to bring the population to its original level.

(c) *Effect of atmospheric and soil temperatures on the activity of soil organisms*

The atmospheric temperatures were taken from the meteorological records of the Rothamsted Station, and the soil temperatures were recorded daily at 9 a.m. on the allotment area at a depth of 8 in. Monthly means were worked out in both the cases. The figures, in the case of atmospheric temperatures, were calculated from the mean of weekly maxima and minima. The two temperature curves are shown in Fig. 7. It will be seen that they almost followed the same course. Attention in the following description is, therefore, confined to one of them, viz. the atmospheric temperature.

The allotment area counts were considered to represent accurately the activities of the soil fauna. The unenclosed controls of this area have, therefore, been selected for this study. No organism or group of organisms occurred so regularly as the Collembola. The effect of the above physical factors is probably more pronounced on this order than on any other.

Fig. 7 shows that from the beginning of February to the middle of September, Collembola maintained a low population of 7·2–24·0 million per acre. During this period the mean atmospheric temperature rose from 35 to 61° F. With the gradual fall of the temperature soon afterwards to 45° F. there was a sudden rise in Collembola till the peak was reached in the middle of November. The temperature continued to fall and reached a minimum of 38° F. in early December. A low range of temperature (38–42° F.) then prevailed up to the

beginning of March. The fall of temperature below 45° F. affected the activities of Collembola, and their density fell to 49·9 million per acre in about a month's time. With the prevalence of low temperature, i.e. 38–42° F., their population remained more or less stationary at 43·6–55·9 million per acre.

Several interesting suggestions brought out by this comparison may be summarized as follows:

(1) When the mean atmospheric temperature rises from 38 to 61° F. during spring and summer, Collembola maintain a low population.

(2) When the temperature begins to fall during autumn, the Collembolan activities increase and are at their maximum during a falling range of 55 45° F. which appears to be the zone of optimum temperature.

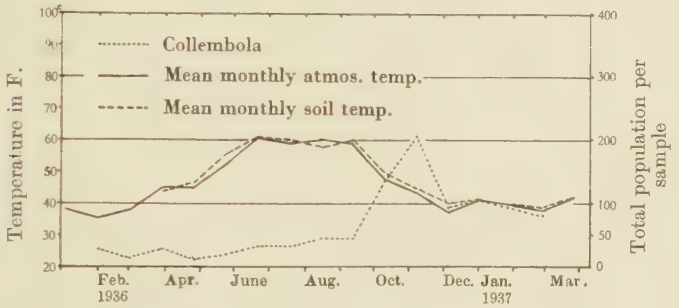


Fig. 7. Effect of atmospheric and soil temperatures on the activity of Collembola.

(3) Temperatures below 45° F. prove inimical to Collembola and their activities are suspended at about 38° F. A further fall below 38° F. is likely to reduce their number.

(4) Since the winter of 1936–7 was comparatively milder than the preceding one, the Collembolan density stood at a higher level. Measuring it in term of highest population figures of the summer months, viz. 24·0 million per acre, it was 1·8–2·3 times more abundant than in the winter of 1935–6.

11. Rate of recolonization of the sterilized plots

(*a*) *Unenclosed plots*

Recolonization in both the instances of sterilization (Table 15, Fig. 8) was much more rapid than was originally expected. The rate of the monthly return of the total soil organisms is worked out below in proportion to the corresponding control. It progressed as follows:

Size of population in relation to the control in months after sterilization

	1	2	3	4	5	6	7	8	9	10	11	13
Sterilization 1	0·15	0·14	0·41	0·31	0·91	0·64	1·08	1·6	1·3	2·6	2·6	2·5
Sterilization 2	0·1	0·26	0·72	0·95	0·8	1·0	2·2	2·4	—	3·6	—	—

The population took 7 months to get beyond the control, and having done so remained far above it, maintaining a density of 2·5 times in sterilization 1 and 3·6 times in sterilization 2 at the end of the observations. The rate in the former was slow for the first four months on account of cold weather, but in the warm weather later on it was very much accelerated. In the second case, since it coincided with the warm conditions, the rate was rapid from the beginning.

Among all other organisms which returned to the sterilized plots (Tables 10 and 11) insects formed, in general, the high proportion of 90–95%, and were

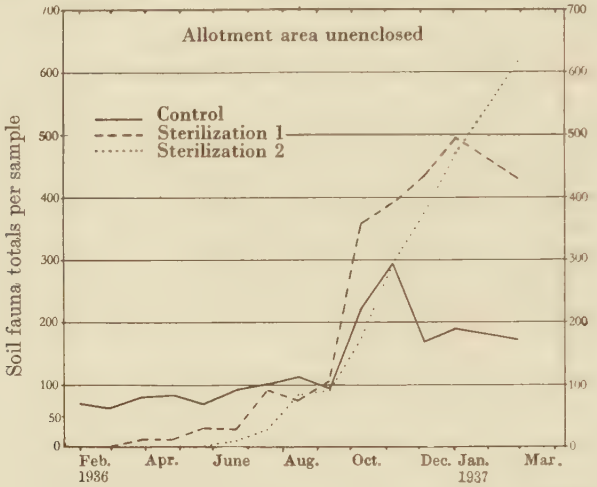


Fig. 8. Rate of recolonization of soil fauna in the unenclosed plots of allotment area.

Table 15. *Recolonization of soil fauna*

Mean date of monthly sampling period	Mean population per sample: Unenclosed plots: Control	Unenclosed plots: Sterilization 1	Unenclosed plots: Sterilization 2	Enclosed plots: Control	Enclosed plots: Sterilization 1	Enclosed plots: Sterilization 2
1936						
1 Feb.	69·6	—	—	47·8	—	—
29 Feb.	62	0	—	45	0	—
28 March	80·7	12	—	101·7	7·5	—
25 April	82·1	11·5	—	107·3	19	—
23 May	70·3	29	0	71·3	12·5	0
20 June	89·8	27·5	9·5	72·6	20	3·5
18 July	100·4	91	26·5	85·0	88	41
15 Aug.	112·1	72	80·5	85·0	117	72·5
12 Sept.	93·8	101	89·5	88·9	136	72
10 Oct.	221	357	176·5	150·5	182	168·5*
7 Nov.	296·1	392	296	289	403·5	430·5
5 Dec.	169·1	433	374	227·0	588·5	318
1937						
2 Jan.	191·4	493	468·5	176·1	714·5	494·5
30 Jan.			No observations made			
27 Feb.	172	428	618	91	423	508

* Excluding a colony of *Trichocera* (?) numbering 454.

mainly composed of Collembola and the immature forms. The percentage of their monthly increase relative to the entire population was as follows:

		1	2	3	4	5	6	7	8	9	10	11	13
Sterilization 1	Insects	50	91	74	73	82	93	79	89	91	91	90	93
	Collembola	21	40	50	40	47	65	56	47	45	53	53	66
	Immature forms	12·5	40	24	22	31	24	19	39	42	36	30	25
Sterilization 2	Insects	68	85	91	92	93	93	91	94	—	96	—	—
	Collembola	10	19	43	49	34	60	61	64	—	66	—	—
	Immature forms	37	51	35	33	56	26	26	28	—	25	—	—

The low percentage of insects in the beginning is due to the large number of other invertebrates; Myriopoda and Arachnida being 41 and 9% in sterilizations 1 and 2, and 21% in sterilization 2 respectively. Among adult insects Thysanura formed 12·5% and Formicidae 4% in the first treatment and Coleoptera 21% in the second. This kept the ratio of Collembola and immature forms low to begin with, but they soon outnumbered the others.

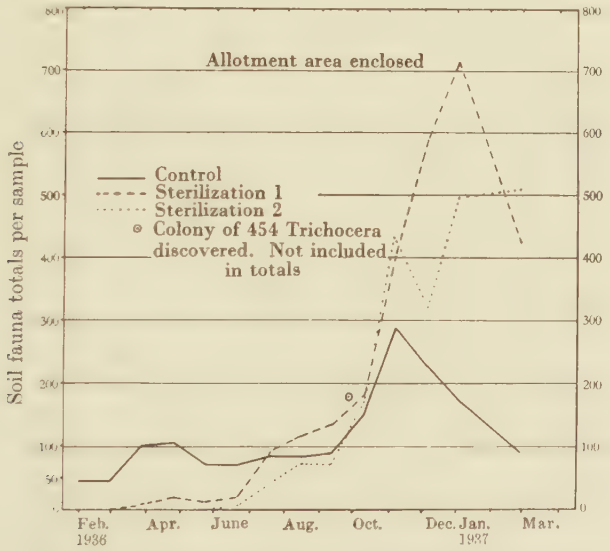


Fig. 9. Rate of recolonization of soil fauna in the enclosed plots of allotment area.

(*b*) *Enclosed plots*

The rate of recolonization (Table 15, Fig. 9) in the enclosed plots was slightly more rapid than in the unenclosed plots. The population density of the control was passed within five months, after which it continued to grow and at the end of the observations had attained a density of 4·6 times in sterilization 1 and 5·58 times in sterilization 2. The rate of recolonization in proportion to control

is worked out below. As in the unenclosed, it was slower for the first four months in sterilization 1 and quicker in sterilization 2 from the very beginning.

	Size of population in relation to their control in months after sterilization											
	1	2	3	4	5	6	7	8	9	10	11	13
Sterilization 1	0·07	0·18	0·18	0·28	1·04	1·38	1·5	1·2	1·4	2·6	4·06	4·6
Sterilization 2	0·05	0·48	0·85	0·8	1·12	1·5	1·4	2·8	—	5·58	—	—

Insects (their chief components being Collembola and the immature forms) constituted a major portion of the entire population (Tables 13 and 14). Their percentage of increase in proportion to the total soil population is indicated below.

		Months after sterilization											
		1	2	3	4	5	6	7	8	9	10	11	13
Sterilization 1	Insects	67	82	76	90	90	89	90	90	92	96	96	95
	Collembola	0	66	48	63	34	63	51	42	59	42	42	32
	Immature forms	7	8	28	25	49	21	21	46	29	49	48	61
Sterilization 2	Insects	100	95	93	90	97	95	94	95	—	98	—	—
	Collembola	14	22	43	56	36	64	55	49	—	60	—	—
	Immature forms	86	66	44	22	58	29	38	45	—	37	—	—

Myriopoda constituted 33%, adult Coleoptera 33%, and adult Formicidae 27% in the beginning of sterilization 1, but did not keep pace with the rapid increase of Collembola. The return, in the case of sterilization 2, was confined to insects alone. The low percentage of immature forms in the first case was due to the passive condition of the insects on account of the prevailing cold.

(*c*) *Comparison of the total population of simultaneous sterilizations*

(1) *Sterilization* 1 (*in February* 1936) *of unenclosed and enclosed plots.*

The return of the organisms in both cases (Fig. 10) was very slow up to the middle of June, and after this with the increased activity, particularly of insects, on account of warmth, the soil began to exercise its attractive influence. The growth of population in the enclosed plots was greater and the ratio between the unenclosed and the enclosed plots in the peak which occurred in January in both cases stood at 1 : 1·4. By about the following March both had come down to almost the same ratio of 1 : 0·99.

(2) *Sterilization* 2 (*in May* 1936) *of unenclosed and enclosed plots.*

The total population in these instances (Fig. 11) followed a similar course. The recolonization was rapid from the beginning, due to suitable warm conditions. The rise of population continued throughout the period of observation, except one month when there was an abrupt fall in the enclosed plots, but was soon followed again by a sharp jump upwards. Unlike sterilization 1 the population of the enclosed stood slightly below the unenclosed plots with a ratio of 1 : 0·8 at the end of observations.

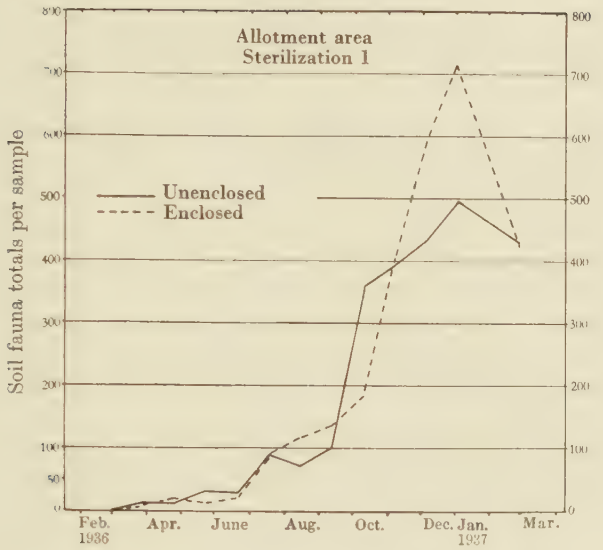


Fig. 10. Comparison of the total soil fauna of sterilization 1 in the unenclosed and enclosed plots of allotment area.

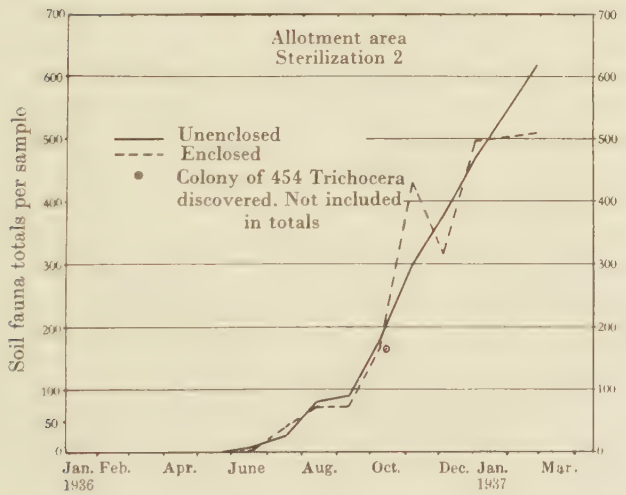


Fig. 11. Comparison of the total soil fauna of sterilization 2 in the unenclosed and enclosed plots of allotment area.

12. Behaviour of some soil population components

Only the predominating or the interesting forms have been selected for this discussion (Table 16). It will be seen that they form 79·6–88·3% of the population. In some cases, for example Collembola, Aphididae, etc., where analysis of individual species was impossible for lack of time, the family has been considered as a whole.

The mean population of each form is in millions per acre, and its percentage is worked out with respect to the total soil fauna (Table 16). The increase is

Table 16. *Behaviour of some soil population components of unenclosed plots in allotment area*

Series no.	Organisms	Control		Sterilization 1			Sterilization 2		
		Mean population in millions per acre	Percentage of total population	Mean population in millions per acre	Percentage of total population	Size of population in relation to control	Mean population in millions per acre	Percentage of total population	Size of population in relation to control
	Collembola								
1	Onychiuridae	14·113	20·9	8·154	8·3	0·6	8·625	7·7	0·6
2	Hypogastruridae	0·836	1·2	15·472	15·7	18·5	18·243	16·3	21·8
3	Entomobryidae	11·029	16·3	17·772	18·1	1·6	24·777	22·2	2·2
4	Isotomidae	7·004	10·4	10·507	10·7	1·5	13·930	12·5	2·0
	Hemiptera								
5	Aphididae	0·073	0·1	0·157	1·8	23·6	3·189	2·9	43·6
	Coleoptera, adults								
6	*Acupalpus meridianus*	0·146	0·2	—	—	—	0·784	0·7	5·4
7	*Amischa analis* Gr.	0·021	0·03	0·366	0·37	17·5	0·261	0·23	12·5
8	*Anommatus* 12-*striatus* Wesm.	0·46	0·7	0·042	0·04	0·1	0·052	0·05	0·1
	Immature forms								
9	*Harpalus* sp.	0·993	1·5	0·057	0·06	0·06	0·026	0·02	0·03
10	*Homalium* sp.	0·031	0·05	0·209	0·21	6·7	0·392	0·35	12·5
11	*Agriotes* sp.	0·016	0·02	0·042	0·04	2·7	—	—	—
	Diptera, immature forms								
12	*Tipula* sp.	0·026	0·04	0·042	0·04	1·6	—	—	—
13	Chironomidae	1·1	1·6	3·764	3·8	3·4	2·875	2·6	2·6
14	Cecidomyidae	3·554	5·3	18·347	18·7	5·2	14·166	12·7	4·0
15	*Sciara* sp.	0·261	0·4	0·522	0·5	2·0	0·549	0·5	2·1
16	*Scaptomyza disticha* Duda	0·136	0·2	1·725	1·8	12·7	4·783	4·3	35·2
	Hymenoptera								
17	Formicidae	0·157	0·2	0·021	0·02	0·1	0·026	0·02	0·2
	Myriopoda								
18	*Blaniulus guttulatus* Bosc.	6·743	9·9	2·352	2·4	0·3	1·333	1·2	0·2
19	Symphyla	0·042	0·06	—	—	—	—	—	—
	Arachnida								
20	Araneida	0·256	0·4	0·34	0·3	1·3	0·444	0·4	1·7
21	Acarina	6·848	10·1	5·332	5·4	0·8	3·816	3·4	0·6
	Total		79·6		88·28			88·07	

reckoned over the corresponding control. It is obvious from the above comparison that, with a few exceptions, the insects increased rapidly in the sterilized plots and went beyond the control. Only Araneida, among other invertebrates, reached the normal density. Some striking cases are dealt with below.

Collembola. Onychiuridae were regularly present in the control throughout the period of investigation, while Hypogastruridae were only absent towards the end of May. The former composed 20·9% of the population and the latter 1·2%. Their behaviour in the sterilized plots was entirely opposite. Onychiuridae failed to regain their normal strength, while Hypogastruridae increased 18·5 and 21·8 times in sterilizations 1 and 2 respectively. Entomobryidae and Isotomidae, which were regularly recovered from the soil, showed an increase of 1·5–2·2 times over the control.

Hemiptera. Aphididae were absent in the control plots up to the middle of July and later they were more or less regularly present; but in the sterilized plots the recolonization was quite marked, starting from the middle of June and continuing till the end of the observations. Their increase amounted to 23·6 times in sterilization 1 and 43·6 times in sterilization 2.

Coleoptera. Beetles occurred as adult as well as immature forms. Nos. 7 and 8 (Table 16) are worthy of some remarks. *Anommatus* 12-*striatus* was present in the controls throughout the period of investigation, with an average population of 0·5 million per acre. It could only regain one-tenth of its normal strength in the sterilized plots. *Amischa analis* on the other hand was recovered once in March in the control and 8 times in sterilization 1 and 4 times in sterilization 2, the relative increase in numbers being 17·5 and 12·5 times respectively.

Harpalus sp. among the immature forms composed a higher population (1·0 million per acre) than *Homalium* sp. (0·03 million) and *Agriotes* sp. (0·02 million); but in the process of recolonization *Homalium* sp. increased 6·7 times in sterilization 1 and 12·5 times in sterilization 2, and *Agriotes* sp. 2·7 times in sterilization 1 and failed to return in sterilization 2; while *Harpalus* sp. only recovered 0·03–0·06 of its original strength.

Diptera. Adults were very uncommon, while immature forms were present in large numbers. Cecidomyidae occurred mostly in over-wintering cocoons. All the Diptera showed a marked increase over the control except *Tipula* sp. which failed to return in sterilization 2. *Scaptomyza disticha* behaved in an interesting manner. It was poorly represented in the controls with an average population of 0·1 million per acre, but its increase in the sterilized plots was very prominent, being 12·7 in sterilization 1 and 35·2 times in sterilization 2.

Hymenoptera. Ants (Formicidae) were encountered in the control in very small numbers, their average population being 0·16 million per acre. During the recolonization process they were discovered once in April in sterilization 1 and once in September in sterilization 2. They thus only succeeded in regaining one-fifth to one-tenth of their normal strength.

Other invertebrates. Among the other invertebrates, Araneida alone succeeded in increasing beyond the control population, while all others failed to regain their normal density. The Myriapod *Blaniulus guttulatus* was a regular soil inhabitant with an average population of 6·7 million per acre in the control. Its rate of recolonization, in the sterilized plots, was strikingly poor. It only managed to recover 0·2–0·3 of its normal strength. Acarina also behaved in the same manner, but their return was a little more rapid. Symphyla occurred occasionally in the controls, but were never found in the sterilized plots.

13. Economic aspect

Sterilization is one of the chief means of pest control inside glasshouses. It increases the soil fertility and, combined with heavy dressings of manure which are not infrequently applied to the plants inside, encourages a luxuriant plant growth. Some of the organisms which gain access to the glasshouses find the new physical conditions favourable and, being protected from their natural enemies, multiply rapidly above and below the surface of the soil, and so assume the status of a pest. The rate of increase of soil animals, particularly insects as already shown, is extremely rapid. Food appears to determine the recolonizing species and sterilization indirectly exerts an influence on their quick return. If, in place of lawn grass, some glasshouse vegetable had been cultivated in the above experiment, the dominating soil organisms would have differed. However, the occurrence of some forms common to the glasshouses and the present experiment is quite interesting.

The springtail *Hypogastrura armata* Nic. is one of the pests of mushrooms inside glasshouses and in the present case Hypogastruridae composed chiefly of *H. armata* Nic. multiplied 18·5–21·8 times over their original strength. A fly, *Sciara* sp., is also another pest of mushrooms. Its increase amounted to double its normal density. Wire-worms, *Agriotes* sp., and leatherjackets, *Tipula* sp., which attack tomatoes in glasshouses, showed an increase of 2·7 and 1·6 times respectively. Aphididae, though not represented by any common species, developed 23·6–43·6 times and it is not surprising to see "root aphis" often occurring on the roots of auriculas and primulas in pots in glasshouses. The Myriapod *Blaniulus guttulatus* did not regain its normal strength, but in presence of strawberry, on which it thrives, its behaviour probably would have been different. These soil organisms might have reacted differently under glasshouse conditions and their number probably would have been much more pronounced. It would be very interesting if such observations could be repeated inside a glasshouse and determinations made as to how soon and in what strength the soil insects or other organisms make their reappearance.

Conditions similar to those in glasshouses are to be met with in tropical countries. The atmospheric temperature during dry summer months is very high and almost sterilizes the soil. Chapman (1931), describing the temperature

of soil communities, remarks: "The annual and diurnal fluctuations of the soil surface on the desert presents probably the greatest temperature fluctuations of any natural environment. Certain Egyptian soils are essentially sterilized each year at the time of the greatest angle of incidence of the sun's rays."

His statement is apparently based on the work done by Taylor & Burns (1924) and Taylor & Williams (1924). While describing the soil temperature observations at Cairo during the "*Sharaqi*" period, Taylor and Burns state: "It may be assumed, therefore, that whenever the minimum screen temperature is 69° F. and at the same time the daily range is 27° F., the soil will become heated to such a temperature that partial sterilization will take place unless some factor other than temperature is introduced to prevent it."

When after such conditions in a tropical country there is a fall of temperature and increase of relative humidity, due to the breaking out of monsoons or excessive irrigation in the following season, conditions very similar to those in glasshouses prevail over a large area. There appears every likelihood of well concealed soil organisms like Collembola and immature forms increasing abnormally and causing damage to field crops. "Root disease" of sugar-cane in Louisiana (Ingram, 1931; Spencer & Stracener, 1930) is attributed in its initial stage to small organisms like *Lepidocyrtus violentus*, *Onychiurus armatus*, etc., followed by the fungus *Pythium*. It is quite possible that the "root rot" of cotton and other field and orchard crops in tropical countries, including India, may be found to originate from the direct damage caused to the tender roots of the young plants by the vast number of these small animals produced during their favourable period of growth. This investigation therefore, in addition, indicates the desirability of research being carried out regarding the recolonization of sterilized soil in the tropics.

14. Comparison of enclosed and unenclosed plots

While it would be unwise to be at all dogmatic about the rate of recolonization in the two sets of plots and the specific nature of fauna recolonizing them, it was, nevertheless, rather surprising that the enclosed and unenclosed plots were recolonized in a similar manner both as regards quality and rate. In fact, the mean population in the enclosed plots was slightly higher in sterilization 1, being 109·0 million per acre against 98·4 million in the unenclosed plots and almost equal in sterilization 2, viz. 110·2 million in the enclosed and 111·8 million in the unenclosed plots.

Three means of recolonization in the sterilized plots were possible: (1) reinfestation from the subsoil, (2) lateral migration, (3) aerial reinfestation.

(1) *Reinfestation from the subsoil.* The soil of Rothamsted, as already pointed out, is sticky clay. A free movement of the soil fauna appears almost impossible. As will be shown under "Subsoil population" (p. 157) ,only a small proportion of the total soil fauna, i.e. 2–14%, exists below 9 in. and possibly

utilize earthworm burrows for their retreat. Besides insects, which formed about half the subsoil population, Myriopoda constituted the major portion of the remaining half. Of the insect population, Collembola (Onychiuridae, Isotomidae and Entomobryidae), formed a concentration up to 4·4%. The remaining orders were Thysanura, Thysanoptera and Psocoptera. Myriopoda failed to regain their normal strength in the sterilized plots, Onychiuridae also lagged behind, Isotomidae and Entomobryidae attained 1·5–2·2 times their original size. The other minor insect orders were poorly represented in the allotment area and their small numerical strength cannot be expected to effect the soil fauna density in the top 9 in. to any appreciable extent. Under these conditions it is difficult to conceive of any considerable reinfestation from the subsoil. If it existed at all it must have been very slight.

(2) *Lateral migration and* (3) *aerial reinfestation.* Having created empty niches in the soil, one would have expected a more rapid influx of the soil organisms in the unenclosed plots owing to the possibility of lateral migration of the soil organisms in addition to the aerial one. The fact that recolonization averaged 5 months in the enclosed plots and 7 months in the unenclosed ones is opposed to such a notion. Taking the percentage composition of the soil fauna (Table 7) it is seen that the insects formed a comparatively higher percentage in the enclosed controls (viz. 71·2%) than in the unenclosed (viz. 66·1%). Immature forms predominated in the former with a composition of 21% as compared to 14% in the latter. Similar differences in the number of the immature forms are also noticeable in the sterilized plots of the two sets, i.e. 39–42% in the enclosed plots and 30–33% in the unenclosed. These forms could not have increased in the enclosed controls unless reinforced from above and also could not have established themselves and exceeded their original numbers in the sterilized plots without the aerial migration. Had there been any considerable lateral movement of the soil organisms, the immature stages in the unenclosed plots would have far exceeded those of the enclosed. Since this phenomenon did not occur, it appears likely that the lateral migration was quite insignificant. More observations are needed to observe lateral movements of the organisms in the soil, but the aerial migration which is quite evident leads once again to a consideration of another aspect of glasshouse horticulture.

The soil inside glasshouses, like that of the enclosed plots, is surrounded by deep impermeable foundations and the aerial atmosphere is congenial to plant and animal growth. An attraction to sterilized soil has been shown to be pronounced at least with some soil organisms. Hence the dangers of soil contamination are greatly enhanced. Possible sources of soil contamination lie in the use of organic manure, tools and appliances, improper use of screens and ventilators, etc. Once an organism is successful in gaining admission to the inside of the glasshouse, it will soon multiply in strength and, its lateral flow being impossible, inflict heavy losses unless counteracted in time. The use of

sterilized soil, as previously shown, will help to stimulate this already rapid rate of increase. It is, therefore, not surprising to see some of the glasshouse pests exacting a heavy toll on the industry almost every year.

It will thus be evident that the use of sterilized soil, though an effective means of improving soil conditions, has some risks. It is possible that under strict precautionary measures, the contamination of the sterilized soil may entirely or to a great extent be avoided, but if ever it occurs and remains unattended, it may result in serious consequences to the industry.

15. Subsoil population

There has been considerable controversy about the subsoil population in almost all the investigations carried out on the soil fauna. Thompson (1924) remarked: "The soil was examined, occasionally, below the specified depth of the routine samples. Under normal or very moist conditions organisms were of rare occurrence below 9 in.; an occasional *Achorutid* was found. As the soil became dry, *Oligochaetes* began to work their way downwards, and when drought conditions held, a few Symphyla and *Achorutidae* and an occasional insect larva occurred at a depth of from 9 to 12 in., but not lower." She was later on supported by Ford (1935) who observed, "Save for an occasional Lumbricid, no organisms were ever found below a depth of 8 in. and in very few below 4½ in." On the other hand, Morris (1927) stated: "In some groups, no individuals were found at a greater depth than 7 in., although from the diagram it seems probable that the Insects, Collembola and 'Myriapoda' occur to a greater depth than 9 in., at least in plots receiving dung." He was followed by Edwards (1929) who asserted: "The tendency of the modern investigations has been to show that the soil organisms do not descend to greater depths during the winter months. The present data suggest that in lighter type of soils the organisms do descend to deeper levels but in heavier type the reverse is the case."

In the light of such inconsistent views it was deemed desirable to study the soil population as far down as possible. The observations were divided into two sets, the first was carried out in May 1936 and the second in January 1937. Three determinations were made in the former and two in the latter. Since it was difficult to cut a profile 2 or 3 ft. deep, the soil was divided into three layers, viz. top to 9 in., 12–21 in., and 24–33 in. deep, the intervening layers of 3 in. being left, in order to avoid mixing of the soil fauna during sampling. Extra care was taken to plug the sampler with cotton wool to avoid other organisms falling into it from the immediate neighbourhood. Table 17 gives the necessary details and Fig. 12 represents their variation.

A glance at the table shows that the soil population in the top 9 in. varied between 80·4 and 90·7% and was higher in spring than in winter, while the reverse was the case in the lower two layers, where it increased almost to

twice its spring strength owing to the migration of the fauna downward on account of thermotropic responses in winter.

The insect population remained higher in all the three layers in winter than in spring, the comparative increase being marked by a difference of 15·9, 4·7 and 4·4% respectively.

In the case of other soil invertebrates, Myriopoda displayed marked variation. Their concentration was appreciably higher in May, probably due to breeding, and decreased by more than one-third in January in the first layer,

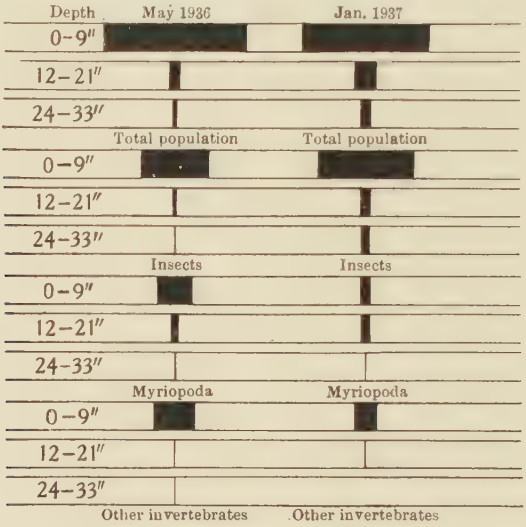


Fig. 12. Depth distribution of soil fauna.

Table 17. *Soil and subsoil population* (%)

Date	Depth (in.)	Insects	Myriopoda	Other invertebrates	Total
May 1936	0– 9	43·4	21·9	25·4	90·7
	12–21	2·2	4·2	0·7	7·1
	24–33	0·95	0·95	0·3	2·2
Jan. 1937	0– 9	59·3	6·9	14·2	80·4
	12–21	6·9	5·6	1·1	13·6
	24–33	5·3	0·7	—	6·0

while it remained almost constant in the bottom two. Besides Myriopoda, all the other invertebrates taken together (in which Arachnida predominated) showed a higher proportion in spring and diminished by about half in winter in the top layer, but maintained a constant ratio in the middle and were absent or practically negligible in the bottom layer in the two seasons.

The subsoil of Rothamsted is sticky clay with a considerable amount of flint. It is hardly likely that any organism can thrive in such anaerobic conditions. Curiously enough, some Lumbricid burrows were traced even below 26 in. and in one instance a worm was dug out at a depth of 24 in. It is, there-

fore, possible for the other soil animals to wander down these mines in pursuit of food.

Two specimens of *Aptinothrips rufus* Gmelin (Thysanoptera) were discovered in each of the second and third layers, and one specimen of *Lepinotus patruelis* Pearm. (Psocoptera) from the second in winter. These delicate insects can hardly be expected to tunnel their way so far down. They must have utilized the earthworm burrows for their retreat.

16. Acknowledgements

In addition to the acknowledgement to some of my colleagues at Rothamsted Experimental Station, Harpenden, who are mentioned in the appropriate place in the text, I am deeply indebted to Sir E. John Russell, Director, for providing me with all the facilities during my two years' stay at Rothamsted; to Dr C. B. Williams, Chief Entomologist, for supervision and guidance throughout this investigation; to Major W. R. S. Ladell for the use of his apparatus, and to other members of the Entomological staff, particularly Dr H. F. Barnes, for encouragement and help whenever needed. I am also grateful to the late Dr W. M. Davies, Advisor in Agricultural Zoology, Bangor, for indentification of my collection of Collembola, and for the same purpose to the members of the Entomological and Zoological departments, British Museum (Natural History), particularly Dr K. G. Blair and his assistants for Coleoptera, Dr F. W. Edwards for Diptera, Messrs H. St J. K. Donisthorpe and G. E. Nixon for Hymenoptera, and Messrs F. Laing and W. E. China for Hemiptera. It is also my privilege to be able to express my gratitude to Mr J. V. Pearman, Bristol, for the identification of Psocoptera, Dr Guy Morison, Aberdeen, for Thysanoptera, Dr S. G. Brade-Birks and his assistant Mr S. W. Rolfe, Wye, for Myriopoda and Dr W. S. Bristowe for Araneida.

17. Summary

1. Previous work on the soil fauna is reviewed. It was chiefly confined to the analysis of the density of the soil organisms in relation to their environmental factors.

2. Four plots (9×9 ft.) on an allotment at Rothamsted Experimental Station, Harpenden, were sterilized to a depth of 1 ft. in February, and four more in May 1936, by baking the soil to 212° F. Two plots of each set were barricaded by iron sheets 12 in. below and 6 in. above ground and the others left unenclosed. One control was provided for every two treated plots. Lawn grass was later sown on all of them.

3. The effect of sterilization on these plots was studied by taking samples at fortnightly intervals throughout the sequence of 14 months. In all 214 samples were examined from November 1935 to March 1937. Ladell's flotation method was used for isolating the soil organisms. Magnesium sulphate solution with a specific gravity of 1·11 was used as floating medium.

4. Mechanical soil analyses and a survey of the flora are given.

5. The prominent components of the soil fauna were (of insects) Collembola, Diptera, Coleoptera, Hemiptera and to some extent Hymenoptera, and (of other invertebrates) Myriopoda, Arachnida and Oligochaeta. The mean population during the experiment in the control plots varied from 61·2 to 67·6 million and in the sterilized plots from 98·3 to 111·8 million per acre. An analysis of the individual orders and immature forms is included.

6. The soil organisms took seven months in the unenclosed and five months in the enclosed plots to reach a normal density. At the end of observations in March 1937 the number on the sterilized plots had increased from 1·5 to 1·8 times that of controls. The size of different important orders with respect to their control is calculated. With the exception of minor insect orders all other went beyond the normal strength, while none of the other invertebrates save Araneida regained their normal density.

7. The relative proportion of the insects to other invertebrates was considerably affected in the area, viz. from 2 : 1 in the controls to 20 : 1 in one of the sterilized plots. Some of the predominating forms like Onychiuridae, *Anommatus* 12-*striatus*, *Harpalus* sp., etc. failed to maintain their dominance in the sterilized plots, while some rare ones such as Hypogastruridae, Aphididae, *Amischa analis*, *Agriotes* sp., etc. increased enormously, a striking instance being that of Aphididae which increased 43·6 times over the control.

8. Distinct fluctuations were another feature of the populations. The peak period in the density of their population occurred in late autumn or early winter in the controls and the first set of the sterilized plots. This was caused by the sudden increase of Collembola which was soon followed by an equally sharp decline.

9. The effect of atmospheric and soil temperatures on the variation of Collembola is noted and it is suggested that their numbers increase during a falling range of temperature in autumn (zone of optimum temperature varying between 55 and 45° F.) and that a succession of several mild winters is likely to increase their numbers, with some resulting injurious effect on agricultural crops.

10. The economic aspects of sterilization inside glasshouses and of the baked soils in the tropics are discussed from an entomological point of view. Since both are subjected to heavy infestation of soil organisms, the desirability of further investigation is suggested.

11. A study of the subsoil population showed that a few organisms existed down to a depth of 33 in. Their percentage density varied between 80 and 91 in the top 9 in., being higher in spring than in winter. The reverse phenomenon occurred in deeper layers.

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EXPLANATION OF PLATE 7

The two lower photos show the experimental plots (*a*) at the time of the first soil sterilization, (*b*) at the end of the experiments, with grass which had been sown, and subsequently mown at intervals to permit of soil sampling. The larger plots are 9 ft. square. The smaller ones in (*a*) were used for some preliminary tests. The apparatus to the right in (*b*) is no part of this experiment. Photo (*c*) shows the soil sampling tool.

THE PROTOZOA OF SOME EAST GREENLAND SOILS

By A. DIXON

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1. Introduction

A series of soil samples illustrating stages of plant colonization was collected by Dr and Mrs H. G. Wager on the British East Greenland Expedition (**2**) in the summer of 1936 from Kangerdlugssuak, Lat. 68° 30′ N.

Previous work on the Protozoa of Greenland soils was done by Sandon (**3**) who examined nine samples collected by Dr Morten Porsild at Disko in the neighbourhood of the Danish Arctic Station. His samples were a variety of types, including among them two black peaty soils. On the whole, these samples were rather poor in Protozoa, and in some respects their distribution was unexpected, e.g. one heath soil yielded 15 species of Protozoa—more than soils which were supporting a more luxuriant vegetation.

Sandon's findings show that the climatic conditions do not make the soils of this region unsuitable for the development of Protozoa, since, among these samples, a garden soil enriched every year with poultry manure yielded 46 species, this being the highest number in any of the samples from his world's survey. This garden sample was very rich in Ciliates and Flagellates, but the high numbers were not made up by the testaceous Rhizopoda, as is the case in the soils described here.

The British East Greenland Expedition's samples were taken to a depth of 4 in. and placed in sterile jars which were subsequently sent to Rothamsted for an examination of the protozoan fauna. The observations made were only qualitative, since the time taken in transport precluded any useful quantitative work.

Four media were used for cultivating the Protozoa: peptone agar, soil extract agar, soil extract and hay infusion, and the cultures were kept under observation for four weeks (**1**).

2. Description of samples

The soils are listed according to the stage of plant colonization. With two exceptions, all of them were collected in the region of Kangerdlugssuak, the base of the expedition. The remaining two samples were peaty soils collected

from Angmagssalik about 200 miles farther south. The numbers of species of Protozoa found in each sample are shown in Table 1.

Table 1. *Number of species of Protozoa occurring in each sample*

No. of sample	Rhizopoda		Flagellata	Ciliata	Total Protozoa
	Nuda	Testacea			
6	2	0	3	0	5
4	1	3	5	2	11
9	5	4	8	1	18
1	2	5	9	3	19
8	3	3	8	0	14
2	7	15	9	10	41
5	6	15	6	5	32
7	5	13	7	7	32
3	9	12	10	11	42
10	10	12	13	7	42
1A	4	8	7	3	22
2A	8	16	10	3	37

Sample 6, 10 August. A dry moraine soil near Miki Fjord, *p*H 7·0, stony and grey in colour and showing the first stages of plant colonization. The soil was damp below 1·5 in., though the surface was dry. A few adult plants were scattered about it at wide intervals, also many seedlings which never matured. The following plants were commonly found: *Luzula spicata*, *L. arcuata*, *Trisetum spicatum*, *Oxyria digyna*, *Saxifraga cernua*, and *S. caespitosa*. Only five species.

Sample 4, 11 July. A deposited glacial silt near Miki Fjord, *p*H 6·8, which came from a platform of rock at the base of the moraine mentioned above and forms another early stage in plant colonization. The locality was very wet and the vegetation consisted of *Salix glauca*, *S. herbacea*, *Saxifraga cernua*, *S. oppositifolia* and moss. Eleven species.

Sample 10, 17 August. Soil from just below the largest ruined house of the Skaergaard Peninsula Eskimo settlement, inhabited 150 years ago, *p*H 5·2. This was a dry warm position with a fairly typical vegetation: *Saxifraga cernua*, *Oxyria digyna*, *Draba alpina*, *Erigeron uniflorus*, *Cerastium alpinum*, *Trisetum spicatum*, *Poa glauca*, etc. Forty-one species.

Sample 9, 14 August. Soil consisting of river sand and plant remains, *p*H 5·6, taken from a small, damp plateau, where the soil was frozen from September to the end of May and was boggy in between. The flora on this site included *Salix herbacea* and *Ranunculus glacialis* in great profusion, and *Oxyria digyna*. Eighteen species.

Sample 1, 7 June; *Sample* 8, 11 August. A dark brown soil from red gabbro rock with vegetable remains, *p*H 5·8. In the spring, when sample 1 was taken, the snow had just melted and the soil was wet and the nearby rocks were green with algae. When sample 8 was taken, however, after two months of hot weather, the soil was dry; the flora here was composed mainly of *Salix glauca*, *Erigeron uniflorus*, *Luzula spicata*, mosses and lichens. Nineteen species in sample 1 and thirteen in sample 8.

Sample 2, 12 June; *Sample* 5, 19 July; *Sample* 7, 11 August. A rich vegetation on Thermometer Hill, *p*H 6·2. This position was 180 ft. above sea-level, facing south, and was under a deep snowdrift all the winter. When sample 2 was taken the soil had been exposed for about ten days but was very damp; on the two later dates it had dried. The vegetation was dense, consisting of a mat of *Salix glauca*, *Empetrum nigrum* and *Vaccinium uliginosum* var. *microphyllum*. In sample 2, 40 species and 30 in each of samples 5 and 7.

Sample 3, 10 July. A very rich vegetation site on the lower banks of Miki Fjord, *p*H 5·6. The soil had dried after the melting of the snow and was completely covered with rich vegetation. Among the numerous plant types found were: *Alchemilla alpina*, *A. glomerulans*, *Erigeron uniflorus*, *Cerastium alpinum*, *Veronica fruticans*, *Bartsia alpina*, *Gentiana nivalis* and *Tofieldia palustris*, with patches of *Salix glauca*. There were 43 species.

The soils from Kangerdlugssuak and Miki Fjord showed a transition from moraine to a type of soil composed chiefly of plant remains, which had a peat-like appearance. The only true peats were collected at Angmagssalik on 21 August:

Sample 1 A, *p*H 4·8, from the bank of the main river. The vegetation was plentiful (consisting of *Campanula rotundifolia*, *Luzula spicata*, grasses, sedges and *Chamaenerium* spp., etc.) and was a typical herb field of the district. The Protozoa, 22 species in all, were characteristic of peat.

Sample 2 A, in the same region, from a peat bog of a depth of at least 4–5 ft., *p*H 4·8. The vegetation was characteristic, mainly *Carex rigida*, *Eriophorum Scheuchzeri*, also *Sphagnum* and other mosses. The sample was taken from the top of a peat hag. This site would always be damp, except when it was actually frozen, as the water table was probably 5–6 in. below the level at which the sample was taken. The protozoan fauna was very rich: 39 species.

3. Protozoa present in the soils

The species of Protozoa found in each soil are recorded in Table 2.

All the amoebae found have been previously recorded from soil; it is perhaps worthy of note that *Hartmanella hyalina* and *Naegleria gruberi*, both very common soil forms, were less widely distributed in these samples than previous work would have led one to expect. The dominant species were *Amoeba actinophora*, *Amoeba* a, which was common in seven of the soils, and *Amoeba radiosa*. The last is probably not a true species and is usually regarded as being a stage in the life history of more than one species of amoeba.

The testaceous Rhizopoda were absent from or scanty in the five soils where the vegetation was sparse, but in samples 2, 3, 5 and 7 where the vegetation was rich they were abundant. They also occurred freely in sample 10; this soil, however, is not strictly comparable with the others since there was an increased nitrogen content at this site owing to the previous presence of men and animals.

Table 2.

Soil Protozoa	Samples 1	2	3	4	5	6	7	8	9	10	1A	2A
Rhizopoda nuda												
Amoeba a Sandon	+	+	+	.	+	.	.	.	+	.	+	+
A. verrucosa Ehrbg.	.	.	+	.	+	.	.	.	.	.	.	.
A. diploidea Hartmann & Nägler	.	.	.	.	.	.	+	+	.	+	.	.
A. striata Penard	.	.	+	.	.	+	.	.	.	.	+	+
A. actinophora Auerb.	.	+	+	.	+	+	+	+	+	+	+	+
A. alveolata Mereschk.	.	.	.	.	.	.	.	+	.	+	.	+
A. annulata Penard	.	+	+	.	.	.	.	.	.	+	.	.
A. albida Nägler	.	.	+	.	.	.	.	.	.	.	.	.
A. fluida Gruber	.	+	.	.	.	.	.	.	.	+	.	+
A. radiosa Ehrbg.	.	+	+	.	+	.	+	.	+	+	.	+
A. vespertilio Penard	.	.	.	.	+	.	.	.	.	.	.	.
Naegleria gruberi (Schardinger) Wilson	+	.	.	.	.	.	.	.	.	+	.	+
Hartmanella hyalina (Dang.) Alex.	.	+	.	.	+	.	+	.	.	+	+	.
Biomyxa vagans Leidy	.	+	+	.	.	.	.	.	.	+	.	.
Nuclearia simplex Cienk.	.	.	.	+	.	.	.	.	+	.	.	.
Acanthocystis aculeata Hertw. & Less.	.	.	+	.	.	.	+	.	+	.	.	+
Actinophrys sol Ehrbg.	.	.	.	.	.	.	.	.	.	+	.	.
Rhizopoda testaceous												
Arcella vulgaris Ehrbg.	.	.	.	.	.	.	.	.	.	.	.	+
Pseudochlamys patella Clap. & Lachm.	.	.	.	.	.	.	.	.	.	+	.	.
Difflugia oblonga Ehrbg.	.	.	.	.	+	.	.	.	.	.	.	.
D. globula Ehrbg.	+	+	+	.	+	.	+	.	.	+	+	+
D. constricta (Ehrbg.) Leidy	+	+	+	.	+	.	+	.	+	+	+	+
Cryptodifflugia eboracensis Wailes	.	.	.	.	+	.	+	.	.	.	+	+
Nebela collaris (Ehrbg.) Leidy	.	.	.	.	.	.	.	.	.	.	.	+
N. dentistoma Penard	.	+	.	.	.	.	.	.	.	.	.	.
Hyalosphenia minuta Cash.	.	.	.	.	+	.	.	.	.	.	.	.
Heleopera sp. Leidy	.	.	.	.	.	.	.	.	.	.	.	+
Cochliopodium bilimbosum Auerb.	.	+	+	.	+	.	+	.	.	+	.	+
Euglypha tuberculata Duj.	.	+	+	.	+	.	+	+	.	+	+	+
E. rotunda Wailes	.	+		.	+	.	+	.	.	.	.	.
E. laevis Ehrbg.	.	+	+	.	+	.	+	.	.	+	+	+
Assulina seminulum (Ehrbg.) Leidy	.	+	.	.	+	.	+	.	+	.	.	.
Trinema enchelys (Ehrbg.) Leidy	+	+	+	+	.	.	+	+	.	+	.	+
T. lineare Penard	+	+	+	.	+	.	+	+	+	+	+	+
T. complanatum Penard	.	+	+	.	+	.	+	.	.	+	.	.
Corythion dubium Paranek	+	+	+	.	.	.	.	.	+	+	+	+
C. pulchellum Penard	.	+	+	.	.	.	.	.	.	.	.	+
Sphenoderia lenta Schlumb.	.	+	+	.	+	.	+	.	.	+	.	+
Lecythidium hyalinum Ehrbg.	.	.	+	+	.	.	+	.	.	+	.	.
Pseudodifflugia fulva (Archer) Penard	.	+	.	.	.	.	.	.	.	.	.	.
P. gracile Schlumb.	.	.	.	+	+	.	.	.	.	.	+	+
Microgromia levipes Penard	.	.	.	.	+	.	.	.	.	.	.	+
Mastigophora												
Cercomonas crassicauda Alex.	+	+	+	+	+	+	+	+	+	+	+	+
C. longicauda Stein	+	.	.	+	.	.	+	.	+	.	.	+
Cercobodo agilis Moroff	+	.	+	.	.	.	.	.	+	.	.	.
Helkesimastix faecicola Woodc. & Lap.	.	+	.	.	.	.	.	.	+	.	.	.
Mastigamoeba sp. F. E. Schultze	.	.	.	.	.	.	.	.	.	.	.	.
Monosiga ovata Kent	.	.	.	.	.	.	.	.	.	.	.	+
Phalansterium solitarium Sandon	.	.	.	.	.	.	.	.	.	+	.	.
Bodo celer Klebs.	.	+	.	.	.	+	.	+	.	+	.	.
B. edax Klebs.	+	.	+	.	+	.	+	.	.	.	+	+
B. saltans Ehrbg.	.	.	.	.	.	.	+	.	.	.	+	+
Heteromita globosa Stein	+	+	+	+	+	+	+	+	+	+	+	+
Spiromonas angusta (Duj.)	.	.	+	.	.	.	.	.	.	.	.	.
Sainouron mikroteron Sandon	+	+	+	+	+	+	+	+	+	+	+	+
Allantion tachyploon Sandon	.	+	.	+	.	.	.	+	.	+	+	+
Proleptomonas faecicola Woodcock	.	.	.	.	.	.	.	.	.	+	.	.
Tetramitus spiralis Goodey	+	+	.	.	.	.	.	.	.	+	.	+

Table 2 (*continued*)

Soil Protozoa	Samples 1	2	3	4	5	6	7	8	9	10	1A	2A
Mastigophora (*cont.*)												
Oikomonas termo Ehrbg.	+	+	+	+	+	+	+	+	+	+	+	+
Scytomonas pusilla Stein	.	.	+	.	.	.	.	.	.	.	.	.
Anisonema minus Sandon	.	.	+	.	.	.	.	.	.	.	.	.
Entosiphon sulcatus (Duj.) Stein	+	+	+	.	+	.	.	+	+	+	.	.
Astasia sp. Duj.	.	.	.	.	.	.	.	.	.	+	.	.
Hexamitus inflatus Duj.	.	.	.	.	.	.	.	.	.	+	.	.
Ciliata												
Holophrya ovum Ehrbg.	.	.	.	.	.	.	.	.	.	+	.	.
Enchelys farcimen Ehrbg.	.	.	+	.	.	.	+	.	.	.	.	.
Lionotus lamella Ehrbg.	.	+	+	.	.	.	.	.	.	.	.	.
Colpoda cucullus O.F.M.	.	.	.	.	+	.	.	.	.	.	.	.
C. steinii Maupas	.	+	+	+	.	.	+	.	.	.	+	.
Microthorax sulcatus Englm.	.	+	.	.	.	.	.	.	.	.	+	+
Cinetochilum margaritaceum Py.	.	+	.	.	+	.	+	.	.	+	.	+
Pleuronema chrysalis Ehrbg.	+	+	.	.	.	.	.	.	+	.	.	.
Balantiophorus elongatus Schew.	.	.	+	+	+	.	+	.	.	+	.	.
B. minutus Schew.	+	+	+	.	+	.	+	.	.	+	+	.
Blepharisma sp., Py.	.	+	+	.	.	.	.	.	.	.	.	.
Strombidium gyrens Stokes	+	.	.	.	.	.	.	.	.	.	.	.
Uroleptus musculus Ehrbg.	.	.	+	.	.	.	.	.	.	.	.	.
U. mobilis Englm.	.	+	.	.	.	.	+	.	.	+	.	.
Gonostomum affine Stein	.	.	+	.	.	.	.	.	.	.	.	.
Oxytricha pellionella O.F.M.	.	.	.	.	.	.	.	.	.	+	.	.
Pleurotricha lanceolata Ehrbg.	.	+	+	.	+	.	.	.	.	+	.	.
Stichotricha secunda Py.	.	.	.	.	.	.	+	.	.	.	.	+
Vorticella microstoma Ehrbg.	.	+	+	.	.	.	.	.	.	.	.	.
V. striata Duj.	.	.	+	.	.	.	.	.	.	.		.

Of the two peat soils, sample 2A showed a large population of testaceous Rhizopods, while sample 1A yielded lower numbers; these results suggest that the amount of organic matter in the soil, rather than the *p*H value, was the factor controlling the distribution of the Protozoa of this group.

The Flagellates obtained from these soils were species common to most soils, as for example, *Cercomonas crassicauda*, *Heteromita globosa*, *Oikomonas termo*, *Sainouron mikroteron* and *Allantion tachyploon*. These were recorded for almost every sample. *Entosiphon sulcatus*, though only occasionally found in soils, appear to be more common in these Greenland samples, as it was found in seven of them. *Bodo edax* occurred in six samples and *B. celer* in four. The other Flagellates recorded were only found in one or two samples (see Table 2).

In the case of the Ciliates no particular species can be described as typical of these soils. The ones found most commonly were *Balantiophorus minutus*, *B. elongatus*, *Colpoda steinii*, *Cinetochilum margaritaceum*, *Pleurotricha lanceolata* and *Uroleptus mobilis*, which are all usual soil types. *Colpoda cucullus*, one of the commonest of soil Ciliates, was only found in one soil.

4. Acknowledgements

My thanks are due to Dr Harold G. Wager of the School of Botany, Trinity College, Dublin, and his wife, who collected these soils and provided the data regarding locality and vegetation.

5. Summary

1. Soil samples from Kangerdlugssuak in East Greenland were examined.

2. The highest number of species of Protozoa occurred in soils producing the richest vegetation.

3. An unusually large number of species of testaceous Rhizopods occurred in non-peaty soils.

4. A large protozoan population was present in soils frozen for nine months of the year.

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ON THE INTRODUCTION AND DISTRIBUTION OF *RANA ESCULENTA* IN EAST KENT

By E. P. SMITH

In the winter of 1934–5 I introduced 12 specimens of the European edible frog, *Rana esculenta* (the Hungarian variety), into a pond beside a running stream in my garden at Stone-in-Oxney, East Kent. The site is an old sea-creek which, in Tudor times, formed a small landing stage; but now, since the sea has receded five miles or more, abuts upon a tract of land where the flats comprising the Walland, Romney and Denge Marshes usurp the place of the salt water. It is a maze of dykes, canals, meres and streams intersecting rich pastures.

I bought the frogs first of all because they are extremely ornamental; their colours vary from a shrill emerald green to a blackish bronze olive. Secondly, I wished to save them from the fate of vivisection; and thirdly, I hoped that they would eat the mosquito larvae with which our still waters abound. These 12 frogs had been kept in cold storage and without food for 18 months before passing into my keeping.

At first nothing happened. When the spring came they sat round the edge of the pond sunning themselves. Then, in May 1935, we discovered their vocal abilities. For weeks on end nobody could sleep on the pond side of the house, and the frogs were becoming a first-class nuisance. Then, in June, two of the largest specimens migrated to a mere about half a mile away; and there set up an unceasing cry to attract their mates to them. This mere had dried up in the drought two years previously, and all the pike in it had died or been caught by hand by the villagers, so, except for an occasional heron, there were no natural enemies. At length, in October 1935, the remaining frogs wandered to the same mere.

My belief is that the first to go went to find a new spawning ground, because they had all mated in the original pond and the fish I keep there (large specimens of roach and golden rudd and golden orfe) had devoured most of the tadpoles. Yet, later in the year 1936, the mere was full of young frogs. During this summer nothing very much happened except that they were all vocal, and the villagers living within half to three-quarters of a mile of the mere began to complain bitterly of the "song". At the same time specimens appeared in Appledore three miles away and connected by a circuitous route of water with the mere.

In May 1937 began what I might call the Great Year of *Rana esculenta*. There was an enormous amount of spawn, and tadpoles and minute frogs were to be seen everywhere. Specimens were located as far away as the Great Lake

at Bedgebury on the uplands 14 miles distant and unconnected by water with the mere. The local suggestion in this case is that the spawn was carried there on heron's legs during the preceding summer, for the frogs seem to be dumb for the first year of their lives. They also appeared at Lydd, nearly 14 miles away (by water) in the opposite direction, but connected by almost continuous dykes with the mere. They were appallingly vocal all through the summer. On warm nights they would give the impression of large armies of ducks contending. Cars would draw up and the occupants get out to enquire what the noise was. The villagers became frantic. They called a parish meeting of protest, and addressed complaints to the Ministry of Health and the M.P. for the Ashford Division of Kent. At this point the Press took a hand. During the "silly season" one newspaper published a long, main-page article, humorous and highly exaggerated, about the singing frogs of Stone-in-Oxney. This resulted in demands for the frogs from all parts. A cunning boy discovered how to catch them and numbers were exported to various places in Scotland, to Sussex and Hertfordshire; while a "line" of about 200 was sold to a firm at Barking Creek to cope with the mosquito plague there. I have not heard whether or not they throve.

But now, in 1938, all has changed. The frogs are still very numerous, far outnumbering the common *Rana temporaria*. But their voices have declined or should I say abated? Their song is no longer a full-throated, virile epithalamium. It has degenerated into a thin, tinny and intermittent lyric. No longer is there any chorusing. The song is isolated. Here and there a frog will croak; but I am sure no villager has lost five minutes' sleep this year during the breeding season.

This change has been startling and inexplicable. I could have understood a gradual decline; but such a sudden stoppage was quite unlooked for. The frogs are still as numerous as ever; but they are silent. Does it forecast their decline? If the song is an essential to their breeding, it must do. On the other hand, the weather has been hot and very dry, and conditions generally extremely favourable. The small frogs are certainly not as numerous as last year. Or do they breed in cycles? and have we entered upon an unproductive cycle?

Last year they looked like spreading over the whole of south England. To-day it seems as if they would quickly die out.

During the last $3\frac{1}{2}$ years I have made certain observations of their habits, etc., and I append them.

(1) *Rana esculenta* is very migratory. There seem to be two periods of migration—a small one in about June when the older adults leave the younger, and a sort of "general post" in October when they all change their habitat and seek winter quarters. They will take up their abode in a small pond for a year, then completely desert it and return there, after an interval of a year or two, in large numbers. For instance, the ponds in my garden which have been deserted since the autumn of 1935 now contain a dozen or more specimens of

varying size. I imagine this is due to their "combing" a pond of insect life and then forsaking it. During their migratory periods they will cover large tracts of waterless land, as much as two miles. They travel, as far as I can make out, by night; and progress by means of three or four jumps and then a rest, and then on again.

(2) As regards distribution, it is safe to say that during the $3\frac{1}{2}$ years since their importation they have covered a square of some 28 miles; but a great deal of this area is connected together by water. I do not regard their appearance at Bedgebury as an instance of normal progression. They must have been carried there somehow in the form of spawn.

(3) They are very powerful swimmers and very powerful jumpers. One, who was caught and tested, cleared 4 ft. 9 in. The legs of this frog measured just under 11 in.

(4) They do not breed or sing till they are fully 12 months old. After that, they go on growing for at least another two years; but I doubt if they reach their full size till they are four or five years old.

(5) They are shy when approached, but intensely curious; and they can be caught by watching where one has leapt into the water because he is certain, if you wait for a few minutes, to come to the surface and put his head out exactly at the spot where he leapt in.

(6) They have an almost ventriloquial power of "throwing" their voices. This has been noted on numerous occasions. You think there is a "songster" within a few feet of you, but you find, by tracking him down, that he may be 100 or 200 yards away. They love noise. A motor mower at work, or even an aeroplane overhead, and sometimes a human being imitating their croak will set them singing. Nothing, however, stills the frog's song so instantly as the appearance of a heron.

(7) They mate in May and June. The male thrusts the female under water, remaining himself with his head and half his body above the surface. At such times they are easily caught. The nuptial embrace seems to last for about two hours.

(8) The immature specimens have more the appearance of little toads than little frogs. The powerful hindlegs develop much later in *R. esculenta* than in *R. temporaria.*

Apparently, early in the nineteenth century, a Mr Berney brought about 1500 specimens from France and Belgium and turned them loose in the Fens near Stoke Ferry; but they are no longer plentiful. In 1843 the same species was discovered in the Cambridgeshire Fens at Foulmire, 30 or 40 miles from Stoke Ferry, where they were christened "Cambridgeshire Nightingales" or "Whaddon Organs". It would appear from this that they do not survive in large numbers in the British Isles, but only in more or less isolated little groups. And I believe that my thriving colony is on its way to such semi-extinction.

REVIEWS

THE JOURNAL OF ECOLOGY

(Vol. 27, No. 1, February 1939)

THE February number of the *Journal of Ecology* consists of 250 pages, including ten papers, various reviews, reports of the 1938 meetings and a list of members of the British Ecological Society.

There are several detailed studies of vegetation, two of which deal with forests: first, a comprehensive analysis of the structure and floristic composition of the Southern Nigerian rain forests by P. W. Richards and, secondly, an account of oakwoods near Killarney by J. S. Turner and A. S. Watt, with reference to the climatic and edaphic peculiarities of the district. Another detailed description of vegetation is that of an area in Spitsbergen (Cape Napier), which was first described sixteen years ago and has now been resurveyed by C. G. Dobbs.

In continuation of his salt-marsh studies (Sections IV and V), V. J. Chapman describes certain soil conditions (chloride content, exchangeable bases and moisture variations), as well as giving details of the salt marsh vegetation, both algal and phanerogamic. Another contribution dealing with coastal biology is a description by T. J. Rees of a community of *Rivularia bullata* growing constantly upon *Balanus balanoides*.

H. Baker and A. R. Clapham contribute detailed observations on the seasonal variation during a period of five years, in the acidity (pH) of three representative woodland soils near Oxford. H. H. Mann describes the weed herbage of slightly acid arable soils at Woburn. A somewhat unusual type of study is one by H. Milton on the occurrence of viable seeds buried in natural grassland and salt marsh soils in Wales. C. J. Dawkins describes the factors influencing the formation of tussocks by *Schoenus nigricans* near Oxford and also gives a statistical analysis of the facts of their spatial distribution. B. N. Singh and K. Das also deal with the statistical analysis of vegetation, in this case a further contribution to their analytical studies of the distribution of an Indian weed flora on fallow soils.

The reviews deal with the *Journal of Animal Ecology*; a book on Spanish soils; papers on soil erosion; African vegetation; forest ecology and bibliography; and a regional survey of the Cambridge district.

W. H. PEARSALL.

SOVIET ECOLOGY

D. N. Kashkarov (1938). *Fundamentals of animal ecology.* (In Russian.) 602 pp., 140 text-figs. Moscow and Leningrad. (No price given.)

This is the second, thoroughly revised and expanded, edition of a previous book by the same author published in 1933 under the title "Environment and biocoenosis" (see *J. Anim. Ecol.* (1933) 2: 128). The present edition differs from the first in many respects, since several chapters have been rearranged and at least one entirely new one has been added, dealing with the ecology of domestic animals and acclimatization problems.

The book has gained greatly from the revision as regards the introduction of many new data and theories. On the other hand, some additions are made in such a way that the logical sequence of the whole work is considerably disturbed and unnecessary repetitions result. Another fault of the book, pointed out in the review of the first edition, was the scanty attention paid to literature on insect ecology. This has been somewhat rectified now, but the great store of valuable ecological facts and ideas to be found in the entomological literature (especially Russian) still remains practically untouched. For example, the whole great problem of parasitic insects is dismissed with a casual statement that they are "interesting in practical respect", and their role in the balance of populations and in biological control is not even mentioned.

The author, in his preface to the second edition, states that the first was written under strong influence of American ecologists, but that in the meantime Russian ecology has made great strides. One would, therefore, expect a much greater emancipation from American ideas and methods than is actually the case, since references to American papers still predominate greatly even over the Russian ones, while British and especially Continental work is definitely left in the background. Merely as examples, it may be mentioned that no reference can be found to the extensive Continental work on the ecology and biocoenoses of moors; to the comprehensive books and papers by A. Landsborough Thomson on bird migration (a subject on which a number of partly obsolete books are quoted); and to numerous recent European works on geographical variation in birds and mammals.

The American influence finds a particularly clear expression in that a definitely subordinate place is given to autecology as compared with synecology. The author definitely recommends the beginning of ecological studies from a biocoenosis and gradually descending to the study of ecological relations of its components. This approach may have some theoretical considerations in its favour, but the fact remains that all the most outstanding achievements of modern ecology are based on intensive studies of a single, or a few, animals in relation to their environment, with other members of the biocoenosis being studied as parts of that environment.

The above remarks should not be taken as an adverse criticism of the book as a whole, but serve merely to point out some minor faults in an otherwise excellent and generally up-to-date treatment of animal (especially vertebrate) ecology.

B. P. UVAROV.

POPULATION DYNAMICS AND DISTRIBUTION

F. W. Bodenheimer (1938). *Problems of Animal Ecology.* 172 pp., 28 text-figures, numerous tables. Oxford University Press. Price 12*s.* 6*d.*

There are three outstanding features about this book: the patience and industry with which so much evidence from the works of the author and his assistants and from the published papers of other investigators has been amassed and concentrated into so small a space; the success which has rewarded a definite attempt to draw together scattered data into a co-ordinated whole by means of laboratory experiment and observation; and the large proportion of the book which consists of figures.

In his Preface the author expresses the opinion that if any real advance in the understanding of vital problems is to be made, the time has now come for some ecologists at least to return to the laboratory in order to consider what conclusions may be reached from a careful examination of the material obtained in the field, and having formulated their hypotheses, to put them to experimental tests. The justification of this point of view is to be found in the account which follows, in the series of six essays making up the book, of the application of such methods to a variety of problems, which in every case has produced results either conclusive in themselves or providing fresh openings for further work.

The influence on various aspects of animal life of biotic and abiotic factors as well as the physiological reactions of the organism itself, is carefully examined and tested. Besides the more obvious question of distribution, such problems as longevity, population growth and structure, biological equilibrium, sex-determination and geographical variation are considered from the experimental point of view, and in each case some solution is found. The author has also attempted to clear up the existing confusion in the use of such terms as "longevity", "biological control" and "biological equilibrium".

Of particular interest, especially perhaps to those concerned with animals as pests or carriers of disease, is the construction of a series of hyperbolae and life charts which together sum up the life-history of a species, indicating the period of time spent in each developmental stage at any temperature, and the succession of generations, periods of aestivation and hibernation, and the time at which the majority of individuals of each generation have reached a given developmental stage throughout the year. The construction of the hyperbolae is

based on the principle that the life-intensity for each species is a constant depending on time and temperature, and when this constant (determined experimentally) and the variations in temperature for any district are known, the local life-history may be calculated with great accuracy. Furthermore, climographs on which favourable and optimal zones of temperature and humidity are marked can be constructed either to explain observed seasonal numerical fluctuations or to calculate those to be expected in any district in which the species occurs.

It is evident that the author himself is particularly impressed by the influence of climatic conditions, especially that of temperature, on the lives of animals, and he has provided good evidence to support his views. Nevertheless he is willing to allow that no one limiting factor can be ascribed to any species, and indeed the book is noteworthy for the small amount of space devoted to the expression of the author's convictions and the large amount of experimental results provided, from which the reader may draw his own conclusions.

It is unfortunate that a book of such valuable biological content should be marred as this is by a series of easily avoided errors, such as the omission of decimal points and the three arithmetical errors in the table at the bottom of p. 54; the transposition of legends referring to two diagrams in Fig. 13, p. 69; the attributing in a substitution on p. 63 of a positive sign to a negative value; and the expression of values actually to be plotted against each other $[1(x)]$ as a product $(1x)$ in Chapter 2. Many of the tables have suffered from excessive condensation and become difficult to follow owing to insufficient explanation or data; the formula for the determination of the intensity of the struggle for existence on p. 72 is at first sight meaningless owing to the omission of a negative sign. An inconsistency causing misunderstanding is the calculation of results correct to one decimal figure from approximations (p. 69). The author recognizes the mathematicophobia of many biologists, and accordingly describes the appearance of the logistic curve followed by the growth of population in *Drosophila* and gives a table of values from which it can be constructed, but there is no illustration of the curve, which would carry more conviction.

In themselves these are all faults which by no means affect the fundamental value of the work, giving rather the impression of hasty correction; but in a book which the author admits and even intends to be difficult, a series of such errors unduly taxes the patience of the reader. There is, however, a more serious fault, where data set out in a table on p. 59 are used in a calculation on p. 58: the calculation is incomprehensible because there is no agreement between the two sets of figures in four cases out of eight, and furthermore, only one of the results shown can be obtained by substituting the figures given in the formula (p. 52) on which this calculation is based.

In fairness to the author it must be stated that this criticism refers chiefly to Chapter 3, and should not be allowed to detract from the value of the book as a whole, which, besides being both illuminating and stimulating, is apparently the only one of its kind available.

ENID NELMES.

BREEDING SEASONS IN MAN AND ANIMALS

(1) **F. H. A. Marshall** (**1936**). *The Croonian Lecture. Sexual periodicity and the causes which determine it.* Philos. Trans. B, 226: 423–56.

(2) **John R. Baker** (**1939**). *The relation between latitude and breeding seasons in birds.* Proc. Zool. Soc. Lond., Ser. A, 109.

(3) **Ellsworth Huntington** (**1938**). *Season of birth: its relation to human abilities.* 473 pp., 104 text-figures, and 2 Appendixes. John Wiley and Sons, Inc., 440 Fourth Avenue, New York, and Chapman and Hall, Ltd., 11 Henrietta St., London, W.C. 2. Price 3.50 dollars.

(1) Dr Marshall has written a very comprehensive review of present knowledge about the reproductive seasons of birds and mammals, dealing more especially with the immediate causes involved. A close correlation between seasonal and sexual cycles is known to exist

in most species, but, although it is generally believed that climatic fluctuations stand in causal relationship to the reproductive activity, the possibility of a pre-established rhythm cannot be ruled out. Considerable attention is paid to the products of the endocrine glands, in particular the pituitary, and to their interrelationships and effects on the gonads. There is a basic internal rhythm of reproduction which depends in the first place on an alternation of periods of rest and activity: the periodic elaboration of gonadal hormones is in correlation with this rhythm.

The most interesting part of this paper deals with the way in which the internal rhythm is regulated according to climatic changes. The author is able to show how environmental factors, of which the most important is light, may completely alter the nature of the internal rhythm, as in the case of Southdown sheep exported from England to South Africa. Immediately after the first lambing in the Southern Hemisphere they change over the time of sexual season and lamb in the southern spring. Light acts as an exteroceptive factor on the nervous system, and thence by way of the anterior pituitary on the gonads. In the case of female mammals the interaction of internal and external factors is not a simple one, for although, in the absence of pregnancy, the ovary alternates regularly between oestrous and luteal phases, when pregnancy occurs the action of the anterior pituitary is changed and it prolongs the luteal period. More normally, however, as in birds and male mammals, the gonads show a rise in activity in correlation with a similar rise in the output of the anterior pituitary.

Marshall pays considerable attention to the part played by the nervous system and the hypophysis in the regulation of the breeding season, and has produced a very thorough review of the main points. He goes on to deal with the phenomena of sexual display and posturing, which he attributes to a selection of those animals which are best able to exercise a mutual stimulation, and thereby secure a more effective synchronization in gonadal activity.

In this paper Marshall has coordinated the literature of a difficult subject in a very clear style, and has also raised a number of points which should provide ample stimulus to both laboratory and field workers. (Further discussion of some aspects of the problem may be found in the review by W. Rowan (1938), Proc. Zool. Soc. London, Ser. A, 108: 51–77).

(2) Dr Baker's paper is an analysis of the breeding season data of a number of birds whose individual ranges cover a wide latitude. There are two main problems. First, the determination, in days per degree of latitude, of how much earlier the breeding seasons occur as one travels away from the Poles; and second, the way in which breeding seasons cross over from one hemisphere to the other. A certain number of species have been carefully selected, and tables have been made to show the times at which they breed in different parts of their range. The breeding season is recorded throughout by the times at which living eggs are found. A long series of diagrams shows exactly the egg-seasons of various groups of birds, and a very ingenious diagram showing the seasonal changes in the position of the sun overhead and in the length of day is so constructed that a tracing of it could be superimposed on the egg-season diagrams. By this means it is at once apparent whether reproduction is occurring during times of lengthening or shortening days, and what is the actual length of the day. Using this method it is found that egg-laying is very rare when the length of day is under 11 hr., but, on the other hand, many birds are laying while the days are shortening, so that neither a long nor an increasing day is necessary for rapid reproduction in birds.

In the latter part of the paper the author enters into a discussion of the immediate factors affecting breeding seasons in tropical and temperate regions. The diagrams show quite clearly that, in the tropics, breeding usually starts before the sun comes overhead. It is unlikely that temperature is an important factor, since, in these regions, the increase is very small. It is more probable that the stimulus from the sun is in the form of its light (both visible and ultra-violet). The rainy season also seems to be of importance as a factor in the breeding of tropical birds. In the case of birds in the temperate zone the main immediate causes are probably temperature and length of day.

One of the most striking and far-reaching results of Baker's analysis is to show that under natural conditions light is only one of the factors concerned in the determination of avian

breeding seasons, and that too much significance may have been attached to the influence of light as a single factor. There is one further point which should be mentioned, namely, the existence of an internal rhythm which certainly affects the time of breeding. The extent to which the factor is effective varies considerably: for instance, some Southern Hemisphere birds living in the Northern Hemisphere may continue to breed at the time of year (on the calendar) when they would normally do so in the Southern Hemisphere, whereas others change over and breed in the northern spring (see Baker & Ranson (1938), Proc. Zool. Soc. Lond., Ser. A, 108: 101–41).

With regard to the breeding of birds whose range crosses the equator, it would be expected from a study of the diagrams (and since the egg-season roughly follows the position of the sun overhead) that there would be two main egg-seasons in the year. This actually happens in quite a number of cases, although most species have a breeding season which is related to the sun either on its southward or on its northward course. There is, however, a great lack of evidence on the breeding seasons of equatorial birds, especially those living just south of the equator.

This very careful analysis by Baker should encourage those who write papers on their observations on tropical birds to make sure that they include careful notes on the breeding seasons, lest their work should have permanent value only as hand-lists for taxidermists.

(3) The papers by Marshall and Baker have shown that our knowledge of the breeding habits and reproductive physiology of a large number of species of birds and mammals is growing, although it is by no means adequate in any one species: the book now under review deals with a subject about which we know even less, and which affects us, as human beings, even more. Prof. Huntington has written an intensely interesting book on breeding seasons in man. The title alone might easily mark his whole work as heterodox, for every zoologist is taught that, with regard to breeding habits, mammals may be divided into three groups: those which only breed at certain times of the year, those whose breeding is susceptible to external influences, and those which breed at any time of the year. It is in the latter group that we are accustomed to class man. Huntington now puts forward the hypothesis that there is an optimum season for human conceptions and births, and that this is influenced by climatic factors. Previously, any slight increase of reproductive activity in man in the spring has only been known from subjective evidence.

This study of the season of birth among large groups of persons in different parts of the world appears to show that seasonal fluctuations in the number of births occur, and that the former are correlated with weather conditions, especially temperature. The analysis of millions of births has been carried out, using records from official documents, from the dates of births in biographical dictionaries, *Who's Who*, genealogical literature and other books of reference, and from the records of schools, hospitals, asylums and prisons (which are listed in an appendix). These data have been worked out in the form of seasonal curves based on the number of births per day in each month, and this is in every case expressed as a percentage of the corresponding average for the year.

The main factors which may influence the seasonal distribution of births are both those which change with the seasons, namely climate, diet, disease and cultural conditions, such as religious fasts or seasonal migrations and vacations; and those which do not change with the seasons, for instance, urbanization, industrialization, non-seasonal migration and the restriction of births. Certain difficulties have been experienced in allowing for the errors introduced by such cultural conditions.

In general there appears to be a basic rhythm, with the maximum of births in early spring in the case of the temperate zones. The data on longevity indicate that a slight change in the season at which children are born makes an appreciable change not only in the length of life, but also in general health and vigour. Further, there is a seasonal variation in the sex ratio at birth, and a correlation between a low sex ratio and favourable climatic conditions. In the first twelve chapters of the book the author is concerned with showing by means of curves based on large numbers of births, that the seasonal distribution of births and its correlation with weather conditions, in particular with the temperature, occurs in most regions of the world.

In the following chapters these conclusions are tested by showing that the effect of environment on physical vigour "ranks with heredity and training as one of the three great factors in determining human capacities". There are, however, difficulties in the way of any clear-cut exposition and these are fully realized by Huntington, who does not try to conceal awkward data. Using the *Dictionary of American Biography*, *Who's Who in America*, and other sources, he gives diagrams showing clearly the season of birth among persons with varying degrees of eminence. Most of these follow the usual curve with a maximum of births in the winter months, January, February and March, and a distinct minimum in the summer, although there are certain exceptional groups in which the degree of eminence seems to vary according to the geographical region.

By classifying the five major occupational groups under the categories of religious leaders, intellectuals, artists, executives and hereditary leaders, and studying the distribution of their births in the four regions, Western Europe, Mediterranean, North America, and Eastern Europe, he finds that the intellectuals, artists, and executives show a marked rise in births round February–March (although the executives' curve is noticeably smoother than the first two), whereas the religious and hereditary leaders, for whom curves are only given for Western Europe, show birth minima in the early spring and maxima in the August–September period! The importance of this particular set of curves seems to lie in the great regularity with which the maxima for births in the intellectual occupations agree with his hypothesis that the weather near the time of conception is closely connected with intellectual capacities.

The examination of the season of birth among persons of eminence has revealed that the annual rhythm in such cases is far more striking than that of the population as a whole. The large amount of material used in reaching this conclusion leaves little doubt as to its validity. This investigation also showed that the season of birth among the criminal and defective classes of any population follows the same type of fluctuation as in the groups showing longevity and eminence. In other words, the more ordinary people in society tend to arise from conceptions showing a fairly well-marked "basic annual rhythm", with its highest point in May for most temperate countries, or in the region of 62° F. for others; whereas in the extreme classes of society the curve of conceptions conforms far more closely to this basic rhythm, and shows a more striking maximum in May.

There therefore exists some correlation between certain temperatures and the number of conceptions, and also a probability that conceptions taking place within this optimum temperature range will give rise to persons differing in abilities or social qualities from the average of the population. In some 80 regions investigated the conceptions tend to reach a maximum at temperatures averaging 62° F. (or 17° C.) for night and day together. The author considers this to be the optimum temperature for conception, and, in support of this, there is further evidence that reproduction increases both when the temperature rises to 62° F. and also when it falls to this level. It may also be significant that Huntington's optimum temperature for conception is about the same as the optimum for physical health in general. Sufficient data are not, at present, available to determine accurately whether light plays an important part in stimulating reproduction in man, and in Huntington's opinion it is of considerably less importance than temperature.

Another problem concerned with the temperature at the time of birth is also discussed. Present-day evidence suggests that the optimum temperature for mental activity is somewhere about 45° F. (or 8° C.). The reason for this is obscure, but it is interesting that the author points out that those children conceived in late spring (at the physical optimum) will be born in late winter at a temperature which, at least in the temperate regions, is in the vicinity of the mental optimum. He suggests that, just as the physical optimum would be an advantage at conception, so also the mental optimum associated with increased mental alertness would originally have been advantageous at the time of birth of unprotected young like those of man.

Although the whole trend of this book is to emphasize the importance of the climatic factors present at conception and birth, this is mainly because this aspect has been neglected by other workers, and the author fully realizes that other factors such as heredity, diet and

mode of life, if taken together, would almost certainly be found to exert a greater effect upon longevity, health, and achievements than the climatic conditions at conception.

The possibilities of a limited season of birth for man are discussed and the initial inconveniences mentioned. The author considers that such an undertaking, resulting in a distinct season of birth in early spring, would, in the long run, be advantageous, although the difficulties of finding an ideal population on which to apply any such regulations are only too apparent.

There are passages in this book where the argument becomes purely teleological, as on p. 8, where we read: "the facts set forth in later pages suggest that man acquired this fundamental rhythm because it favoured the survival of the young". However, this criticism in no way detracts from the value of a book which puts forward so many important points based on an immense body of data. It is, of course, inevitable that many will pick on the arbitrary way in which the author has been forced to judge longevity or achievements, but at the same time these difficulties will make the reader realize the great need for more far-reaching statistical records on human populations.

In the present state of our knowledge on human reproductive activity very little, if anything, is known of the actual physiological effects of the various proximate factors affecting reproduction, and the value of Huntington's book, although extremely difficult to assess at the present moment, seems to lie in two directions. First, he has synthesized his data into an intelligible form, and in so doing has not been afraid to use sources of information which are unorthodox. In the second place, he has shown quite clearly that we must recognize climatic conditions at the time of conception and birth as factors which may be just as important as heredity and training in conditioning the future man or woman.

H. G. VEVERS.

A CALIFORNIAN BIRD POPULATION

Mary M. Erickson (1938). *Territory, annual cycle and numbers in a population of wren-tits* (Chamaea fasciata). University of California Publications in Zoology, vol. 42, no. 5: 247–334, 6 plates, and 16 text-figs. University of California Press, Berkeley, California. Price $1.25.

This is a competent and interesting report of a bird population study by means of coloured rings. The chief interest resides in the fact that the species under consideration, the intermediate wren-tit (*Chamaea f. fasciata*), a sort of ecological analogue of our Dartford warbler, is completely resident, whereas other species worked on by Howard, Nice and others have been mostly migrants.

The habitat and the method of working are first described. Sight identification by means of the coloured bands was employed mostly during the spring and summer, while in the autumn and winter live trap lines were laid, and records obtained from these. The work was begun in 1931 and carried on intensively through 1932 and 1933.

A long discussion on territory describes how an area of 16·7 acres of homogeneous chaparral is occupied by just under 20 pairs of birds, each territory averaging about 0·8 of an acre in extent, variations in size being largely determined by the amount of boundary that has to be defended. Both males and females stay strictly in their territories for practically the whole of the year, some slight relaxation occurring only during the late summer. Thus there is no taking up of winter territories, as in the case of the European redbreast. The young stay in somewhat ill-defined areas about the margin of the breeding grounds until they are either eliminated or absorbed into the breeding stock as vacancies occur.

Another long section deals with the reproductive cycle, though little attention is given to the factors which are responsible for the onset of reproductive behaviour or the way in which the day-to-day routine is modified in the pre-nest-building stage. It is shown that clutches vary in size both with the time of year at which they are laid, and with the age of the female. There appears to be considerable loss both before hatching and before fledging, and more

data upon this aspect would have been welcome; but it appears that the nests were not very easy to find.

In contrast the vital statistics showing the rate of replacement in the population are full and interesting. The average age of birds which have survived their first winter is shown to be 4·43 years, though one male was known which occupied a territory for 10 years. Thus about a fifth of the population was replaced every year and the age distribution showed a large percentage (61) of birds that were 3 years old or over.

The whole paper is a valuable contribution to knowledge of the population dynamics of vertebrates, and illustrates the important uses to which ringing may be put, in addition to the mere indiscriminate marking of migrants which is so popular a recreation in this country.

H. N. SOUTHERN.

FLIGHT

C. Horton-Smith (1938). *The flight of birds.* 182 pp. 17 plates and 30 text-figs. H. F. and G. Witherby, Ltd., 326 High Holborn, London, W.C. 1. Price 7*s.* 6*d.*

This is an avowedly popular account of the main problems involved in bird flight and a certain amount has been sacrificed to easy writing. However, the chapters which are devoted to the mechanical principles concerned and the methods by which birds make the utmost use of their medium are lucid and avoid too great use of technical terms.

A brief summary is first given of the history of investigations into flying principles, and this is followed by a recapitulation of the structural and physiological adaptations to flight found in birds and the origin of the flying habit. There is nothing very new in this; in fact the important work of Steiner on the last problem is neglected.

The third chapter deals with the variations in the structure and function of birds' wings, and discusses the division of them into those of high and low aspect ratio. Some remarks on the relation of these types to habitat are interesting to the ecologist: birds with long, thin wings are chiefly confined to open country, whereas those with blunt wings are found both in closed and open country. The necessity for rapid almost vertical rising in e.g. woods involves a short broad wing, generally slotted, a high energy output, and the ability to rotate the wing laterally. The question of the camber of a wing and the way in which it gives a greater proportion of lift over drag is also discussed here.

Chapter IV on the flight habit endeavours, not very clearly, to divide the types of flight according to the method of feeding, but the next chapter on gliding and soaring contains much of interest, and explains the particular conditions of climate and wind that are essential for this type of flight. Flapping flight is next dealt with in some detail, and figures are given showing that the relative weight of the pectoral muscles to that of the body is greater in birds which flap their wings quickly than in "sailing" fliers; also that in the former the ratio of wing span to body length is less than in the latter.

Final remarks deal with the velocity of flight, giving rough instructions for making estimations; and with safety devices such as the slotted wing-tip which saves the bird from stalling when the angle of incidence becomes high. Some of the plates are not very successful as pictures, but most of them illustrate their points well enough. A glossary and bibliography are appended.

H. N. SOUTHERN.

ISLAND LIFE

R. M. Lockley (1938). *I know an island.* 300 pp., 17 maps and diagrams and 49 photos. George G. Harrap and Co., Ltd., 182 High Holborn, London, W.C. 1. Price 10*s.* 6*d.*

Islands have a double interest to the ecologist because they form comparatively finite units of life and because many of them, especially in the British archipelago, contain peculiar races and species of animals that differ from those of the mainland and often represent

remnants of ancient populations now disappeared elsewhere. In recent years there has been a great growth of interest in these islands, represented by expeditions of individuals and of University groups who have done primary surveys, especially on the islands of the West of Scotland.

We can now say that the faunal peculiarities of small islands round our coast are shown mainly in the small mammal species, and to a lesser extent in the birds, also in the absence from islands of certain common mainland species. But the invertebrate fauna shows comparatively little insular racial development, a situation we may now understand in the light of Hardy and Milne's discovery of the large amount of small animal life that is dispersed by aerial currents. It seems therefore that mass collecting on islands, such as has been practised by recent expeditions, should give place to a deeper study of island population interrelations, for it is here that the island offers its chief scientific interest to the ecologist.

That there is also a strong aesthetic pleasure to be gained from quiet study in these surroundings, with their peculiar combination of sea and land, of completeness and isolation, and of immunity from human disturbance, will already be realized by many. This book successfully communicates that feeling to the reader, and at the same time gives him a very interesting introduction to the conditions on some West European islands, illustrated by first-rate photographs and good maps.

Mr Lockley's primary interest is in birds, and his headquarters on Skokholm in South Wales, where he has organized some important field investigations on bird life. This wider survey includes many out-of-the-way islands, and is illuminated by acute observations on the environment, the life of the inhabitants (where there are any), and the wild animals and plants. We have Skokholm (with its huge colonies of puffins and other sea-birds); Grassholm (famous for its gannetry); Ramsey (a breeding place of seals); Bardsey; the Blaskets (off Kerry); Heligoland (with the German bird migration station); Fair Isle (originally Faeroe—Sheep Island; another breeding place of grey seals); North Ronaldshay (in Orkney); the Faeroes; and the Westmann Islands (off Iceland). Those who read and enjoy (as they certainly will) this book will learn to look on islands and their inhabitants with a new respect and discrimination which will, it is hoped, help to counteract the tendency for visitors to have a solely spoliating mentality.

CHARLES ELTON.

FRESH-WATER ANIMALS

Helen Mellanby (**1938**). *Animal life in fresh water: a guide to British fresh-water invertebrates.* 296 small pp., 211 text-figures. Methuen and Co., Ltd., 36 Essex St., London, W.C. 2. Price 8*s.* 6*d.*

Here is a serious attempt by a trained zoologist (the author is attached to the Department of Zoology in the University of Sheffield) to provide for schools and for the amateur naturalist a reliable general guide to the invertebrate animals likely to be met with in fresh water. For many years there has been a need for such a book, and many English students have begun by using the American text-book by Ward and Whipple as a substitute.

The treatment is systematic, and the usual method is to describe the characteristics of each family and to give an indication of the further subdivisions within it. There are clear illustrations, mostly original, representing various stages in development, as well as the adults. The degree of detail seems to have been determined by space rather than by logic: there is differentiation between the various species of sponge, hydra, planarian worms and leeches. In other groups the division runs to genera (as with oligochaete worms, Mollusca). The insects are dealt with more briefly still.

The chief criticism one can make of the book is the absence of a good bibliography which would enable the student to follow up any group he is interested in. There are some misprints (as *Gammarus drebeni* for *duebeni*). But on the whole this book can be recommended as a good introduction, and it obviously contains in a highly condensed yet readable form the results of much labour and first-hand knowledge.

CHARLES ELTON.

NOTICES OF PUBLICATIONS ON THE ANIMAL ECOLOGY OF THE BRITISH ISLES

This series of notices covers most of the significant work dealing with the ecology of the British fauna published in British journals and reports. Readers can aid the work greatly by sending reprints of papers and reports to the Editor, *Journal of Animal Ecology*, Bureau of Animal Population, University Museum, Oxford.

Copies of these abstracts are issued free with the *Journal*. They can also be obtained separately in stiff covers, printed on one side of the page to allow them to be cut out for pasting on index cards, by non-subscribers, from the Cambridge University Press, Bentley House, N.W. 1, or through a bookseller, price 3*s*. 6*d*. per annum post free (about 300 notices, in two sets, May and November).

Abstracting has been done by H. F. Barnes, D. H. Chitty, M. Dunbar, C. Elton, F. C. Evans, B. M. Hobby, M. Mare, Barrington Moore, E. Nelmes, F. T. K. Pentelow, H. N. Southern, H. G. Vevers and U. Wykes.

Within each section the groups are arranged in the order of the animal kingdom, beginning with mammals (in the section on parasites the hosts are classified in this order). Papers dealing with technical methods are dealt with in the appropriate sections.

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1. ECOLOGICAL SURVEYS AND HABITAT NOTES

(*a*) MARINE AND BRACKISH

See also **57, 88**

1. Dep. Sci. Industr. Res. (1938). "Estuary of the river Mersey. The effect of the discharge of crude sewage into the estuary of the river Mersey on the amount and hardness of the deposit in the estuary." 337 pp. (London: H.M. Stationery Office. Price 30*s*.)

A very full account of the physics and chemistry of the formation of mud banks. Few biological data are included, but the occurrence of burrowing forms such as *Macoma balthica*, *Nereis diversicolor*, *Pygospio elegans* and *Corophium volutator* was used as an indication of the age and permanence of the banks.

2. Fischer-Piette, E. (1936). "I. Études sur la biogéographie intercotidale des deux rives de la Manche." J. Linn. Soc. (Zool.), 40: 181–272.

Sessile species were examined at 91 stations along the two coasts. Some species, e.g. *Corallina officinalis*, tend to become abundant at parallel positions on the two coasts. As a whole the species fall into six categories: (1) common at all stations visited, e.g. *Patella vulgata*; (2) types dependent on rock surfaces, e.g. *Patella depressor*; (3) those common at one end of Channel and becoming progressively less abundant, e.g. *Chthamalus stellatus*, common at west end; (4) those abundant in exposed situations, e.g. Algae; (5) those abundant in sheltered situations, e.g. *Mytilus edulis*; (6) capricious species, e.g. *Actinia equina*.

3. Hammond, C. O. (1938). "A broadland calamity." Entomologist, 71: 174–5.

In February 1938, Hickling Broad, Horsey Mere, was completely covered by sea water through a breach in the sea wall. Fresh-water fish perished in thousands and all the birds have left, the bittern being the last to go. The rich dragon-fly fauna has been completely wiped out.

4. Holmes, P. F. & Pryor, M. G. M. (1938). "Barnacles in Horsey Mere." Nature, Lond. 142: 795–6.

Balanus improvisus was found in large numbers on the stems of reeds in Horsey Mere, Norfolk, in July 1938. The water has been very saline since the sea broke through in the spring, to which occurrence the presence of the barnacles is presumably due. The fauna of the area is now a mixture of brackish and fresh-water species. *B. improvisus* is a very euryhaline species, occurring in Holland in water of salinity as low as 1·65 per mille.

5. Howes, N. H. (1938). "A brackish water community near Southend." Essex Nat. 26: 104–7.

An artificial lagoon created by the damming of a creek of the River Roach showed a predominantly sea water fauna. The salinity varied from 21 to 28 per mille and is falling by 1 per mille annually. The present fauna contains 2 genera of Protozoa, 6 of Coelenterata, 1 Nemertine, 4 Annelida, 13 Crustacea, 5 Insecta, 6 Mollusca, 1 Polyzoan and 6 vertebrates. Subsequent selection may give precedence to euryhaline species, e.g. *Palaemonetes varians*, *Platichthys flesus*, while the proportions accidentally shut off may influence the future fauna. (For observations on plants and chemical conditions see also **N. H. Howes** (1937). Proc. Linn. Soc. Lond.: 49–51.)

6. Yonge, C. M. (1937). "The biology of *Aporrhais pes-pelecani* (L.) and *A. serresiana* (Mich.)." J. Mar. Biol. Ass. U.K. 21: 687–703.

An account of the habits, habitat and feeding of these two burrowing Gastropod Molluscs.

7. **Fisher, N. (1937).** "Notes on the British Opisthobranchs. 1. The ecology of *Archidoris flammea* A. & H." J. Conch. 20: 362–8.

8. **Brown, R. S. (1938).** "The anatomy of the Polychaete *Ophelia cluthensis* (McGuire)." Proc. Roy. Soc. Edinb. 58: 135–60.

Contains a preliminary section on habits and distribution.

9. **McMillan, N. F. (1938).** "Marine sponges from N.E. Ireland and Co. Dublin." Irish Nat. J. 7: 44–5.

Records of 15 species include brief field notes on colours of the living animals and in some instances their habitats. A new species of *Axinella* is to be described.

(*b*) Freshwater

See also **3, 4, 46, 52, 58, 59, 88, 125, 183**

10. **Dep. Sci. Industr. Res. (1937).** "Survey of the river Tees. Part 3. The non-tidal reaches—chemical and biological." Tech. Pap. Wat. Pollut. Res., Lond. No. 6: 1–189. (London: H.M. Stationery Office. Price 12*s.* 6*d.*)

An account of a chemical and biological survey of the Tees carried out from 1929 to 1933. Contains extensive floristic and faunistic data, in many cases quantitative. The animals and plants are considered as communities and the effect of sewage pollution on the general ecology of the river is discussed. There is an account of the fisheries, and data on the food of fishes are included. There are also accounts of the chemical and bacteriological processes of the decomposition of sewage and of the chemistry of river water.

11. **Kaufmann, R. R. U. (1938).** "The aquatic Coleoptera of the environs of Pannal Ash, near Harrogate. Part I. Hydradephaga." Ent. Mon. Mag. 74: 245–9.

List, with some ecological details.

12. **Browne, F. Balfour- (1938).** "The aquatic Coleoptera of North and South Lincolnshire." Ent. Mon. Mag. 74: 223–32.

An exhaustive list with interesting ecological details.

13. **Browne, F. Balfour- (1938).** "The aquatic Coleoptera of Ross and Cromarty (East and West Ross), including an *Octhebius* new to Britain." Scot. Nat.: 129–34.

A list of all species so far recorded for the district (50 for East Ross; 17 for West Ross).

14. **Walton, G. A. (1938).** "The British species of *Micronecta* (Corixidae, Hemipt.)." Trans. Soc. Brit. Ent. 5: 259–70.

Includes distributional records and some biological information.

15. **Mosely, M. E. (1938).** "The spinner and its eggs. Observations on the habits of egg-laying spinners and the hatching of their eggs." Salm. Trout Mag. No. 90: 18–23.

Egg-laying habits of Ephemeroptera. Specific identifications are not given.

16. **Boycott, A. E. & Oldham, C. (1938).** "The Mollusca of the Brecon and Newport and other detached or isolated canals." Proc. Malacol. Soc. Lond. 23: 33–50.

Canal building as an ecological experiment. A study of the Mollusca of the isolated canals of the west country, and a comparison with those of the main canal basin. The presence or absence of the commonest basin species in the isolated canals is taken as a measure of the overland dispersion which they have achieved in the last 100 years.

(*c*) Land

See also **53, 86**

17. **Flintoff, R. J., Harrison, D. & Mackley, C. (1938).** "Notes on the Hole of Horcum, Saltersgate, North Yorkshire. VI. The Mammalia, Reptilia, and Batrachia." Northw. Nat. 13: 83–92.

The species are listed with notes on abundance, feeding habits and comments of general interest.

18. **Gordon, A. (1938).** "The bats of Helmsley, North Yorkshire." Northw. Nat. 13: 19–21.

Eight out of the twelve British bats have been found within a few miles radius of Helmsley. Two are especially interesting, *Barbastella barbastellus* which is new to the county and *Rhinolophus hipposideros minutus* which was thought to be extinct in Yorkshire.

19. **Whittaker, I. (1938).** "Birds of a Lancashire cotton town: being notes on the avifauna of Heywood." Northw. Nat. 13: 136–44.

Supplementary notes to the 1934 publication of this name. The long-eared owl and little grebe have been added to the list of nesting species.

20. **Wild, S. V. (1938).** "The environments of yellow buntings' singing stations." Northw. Nat. 13: 8–10.

The singing stations of 109 yellow buntings were noted in Cheshire, Staffordshire and the Isle of Man during 1937. The major part of the observation districts is devoted to "mixed" farming. Data show that the birds have a slight preference for root rather than grain crops, but by far the most favoured environments were those least cultivated, i.e. pasture and "waste" land.

21. **Stelfox, A. W. (1938).** "The birds of Lagore about one thousand years ago." Irish Nat. J. 7: 37–43.

More than 1000 bird bones were recovered from a kitchen-midden in swamp land of Co. Meath. About 30 species were certainly or tentatively identified; these were largely water-frequenting birds and scavengers, but also included a primitive breed of domestic fowl and a number of species now rare in Ireland. Vertebrae were almost completely absent from the collection. A plea is made to archaeologists to preserve all small bones recovered.

22. **Jary, S. G. & Stapley, J. H. (1937).** "Investigations on the insect and allied pests of cultivated mushrooms. IX. *Tyroglyphus dimidiatus* Herm. (*longior*) Gerv." J. S.-E. Agric. Coll. Wye, 40: 119–29.

Includes the method for the preparation of specimens by means of KOH and Berlese mounting media.

23. **Austin, M. D. & Pitcher, R. S. (1937).** "Investigations on the insect and allied pests of cultivated mushrooms. X. *Sciara variens* Johns., its occurrence within a mushroom house, with a description of the male genitalia." J. S.-E. Agric. Coll. Wye, 40: 98.

24. **Austin, M. D. (1937).** "Investigations on the insect and allied pests of cultivated mushrooms. XI. The long-legged mushroom mite (*Linopodes antennaepes* Banks)." J. S.-E. Agric. Coll. Wye, 40: 115–18.

25. **Jary, S. G. (1938).** "Investigations on the insect and allied pests of cultivated mushrooms. XII. Two more Tyroglyphid mites." J. S.-E. Agric. Coll. Wye, 42: 66–81.

26. **Massee, A. M. (1938).** "Notes on some interesting insects observed on fruit trees in 1937." Rep. E. Malling Res. Sta. 1937: 203–8.

Many unusual host plant records including the following: the Lamellicorn, *Sinodendron cylindricum*, on healthy cherry trees; the flea beetle, *Derocrepis rufipes*, on apple foliage; the shot-hole borer, *Anisandrus dispar*, on Himalaya blackberry; the weevil, *Epipolaeus caliginosus*, on hop roots; the Clavicorn, *Librodor hortensis*, on mummified apples; the puss moth on apple. Also evidence of a partial second brood of codling moth.

27. **Massee, A. M. (1938).** "Coleoptera associated with cultivated fruits." Trans. Soc. Brit. Ent. 5: 223–34.

About 70 species occur on the various sorts of fruits grown in this country, of which a few are found exclusively on apple, pear, plum, etc., but the majority have other host plants besides cultivated fruits. The number of species recorded on fruit has not varied to any extent during the past 40 years, but a few species are more plentiful now than formerly.

28. **Donisthorpe, H. (1938).** "Coleoptera taken at Muckross, near Killarney, in May." Ent. Rec. 50: 92–4.

Includes some ecological notes.

29. **Donisthorpe, H. (1938).** "A preliminary list of the Coleoptera of Windsor Forest." Ent. Mon. Mag. 74: 259–70.

The concluding part of this serial publication. The complete list now includes 1870 species. Some of these, such as *Bembidium 4-pustulatum* and *Aulonium trisulcum*, etc., have increased enormously in numbers in the last few years; others have become very rare and have not been met with for a long time in the forest.

30. **Wright, A. E. (1938).** "Natural habits of *Hydriomena* (*Perizoma*) *taeniata* Steph. (Lep., Geometridae)." Entomologist, 71: 198–200.

A local moth occurring sparingly about the head of Morecambe Bay in both Lancashire and Westmorland, and inland as far as Witherslack and Windermere.

31. **Cooper, B. A. (1938).** "Further notes on *Tyria jacobaeae*." Entomologist, 71: 263–4.

Discusses emergence date and food plant selection of cinnabar moth.

32. **Freeman, P. (1938).** "Notes on Orthoptera observed in 1937." Ent. Rec. 50: 4–5.

Collecting notes on grasshoppers with some ecological details.

33. **Freeman, P. (1938).** "The distribution of *Metrioptera roeselii*, Hagenb. in Essex in 1937." Ent. Rec. 50: 7–8.

An account of an attempt to map the range of this very local grasshopper.

34. **Wilson, G. Fox (1938).** "The glasshouse leaf-hopper, *Erythroneura pallidifrons* Edw." J. R. Hort. Soc. 63: 481–4.

An account of the insect, its food plants and life history, together with an outline of control methods for infestations under glasshouse conditions.

35. **Davies, W. Maldwyn (1938).** "The aphis *Myzus persicae* Sulz in selected districts of Scotland." Scot. J. Agric. 21: 249–58.

It was recorded from sea-level up to the highest centre visited (850 ft.) and was common both in the north and south. The highest populations occur most frequently at low altitudes and in sheltered gardens in urban areas. High aphis counts on forms in exposed situations or remote from villages were apparently due to the proximity of swedes and other cruciferous crops. The migration of winged aphids to potatoes in June is, in general, determined by the occurrence of days when the maximum temperature exceeds 65° F., the relative humidity is less than 75% and the wind velocity less than 5 m.p.h. The general trend of aphis migration in eastern Scotland is from the west towards the east, since the gentle breezes at the time of these requisite conditions come from the west. In north Wales similar suitable breezes were found to come from the east.

36. **Massee, A. M., Greenslade, R. M. & Duarte, A. J. (1938).** "Notes on the strawberry aphid (*Capitophorus fragariae* Theob.)." Rep. E. Malling Res. Sta. 1937: 209–12.

Life cycle and ecological notes. It can live all the year round on strawberry and under certain conditions on silverweed.

37. **Anon. (1937).** "The chrysanthemum midge." J. Minist. Agric. 43: 1158–61.

The suggestion is made that the midge attacking greenhouse *Chrysanthemum* is distinct from the species attacking wild *Chrysanthemum* species, including the ox-eye daisy.

38. **Beresford, D. R. Pack- (1938).** "Some new and rare Irish spiders." Irish Nat. J. 7: 51–3.

The occurrence of four species new to Ireland and additional records of six other rare species supplements a previous list by the same author.

(*d*) Small islands

See also **80, 178**

39. **Atkinson, R. (1938).** "Natural history notes from certain Scottish islands —North Rona, the Flannan Isles, Handa Island." Scot. Nat.: 145–7.

Notes on the numbers of birds seen during the summers of 1935 and 1937. There is great wanton destruction annually of bird life and seals, black-backed gulls being untouched. The remains of ten species of birds were found in the carcasses and droppings of these gulls.

40. Stewart, M. (1938). "Natural history notes on certain Scottish islands. Sule Stack, Sule Skerry, North Rona, Sula Sgeir and St. Kilda." Scot. Nat.: 107–14.

Notes on the variations in numbers of birds (especially gannets, puffins, kittiwakes, and fulmars) with suggestions for the causes. There are a few topographical and habitat notes. Grey seals, rabbits, earwigs and wood-lice are also noted on Sule Skerry, and mice on St Kilda. There are two maps.

41. Elton, C. (1938). "Notes on the ecological and natural history of Pabbay, and other islands in the Sound of Harris, Outer Hebrides." J. Ecol. 26: 275–97.

These notes describe the vegetation, with evidence of former woodland, the natural conditions, past and present, and history of human occupancy in relation to the present animal life on the islands and in adjacent waters. Pabbay had a large human population until about 100 years ago.

42. Campbell, J. L. (1938). "The Macrolepidoptera of the Parish of Barra." Scot. Nat.: 153–63.

A list of 131 species (69 Noctuidae) recorded between 1935 and 1937 in the Civil Parish of Barra which includes some small islands. The Noctuids were collected chiefly by sugaring, and at sallow, stock, elder and ragwort. Car head-lamps were also used, but a light trap met with little success.

43. Harrison, J. W. Heslop (1938). "A further occurrence of *Zygaena achilleae* Esp. in the Inner Hebrides." Entomologist, 71: 175.

Cocoons of Zygaenid moths from Eigg and Muck yielded *Z. filipendulae* while three *Z. filipendulae* and one *Z. achilleae* were bred from the Eilean nan Each group. *Z. filipendulae* is also recorded from Skye.

44. Harrison, J. W. Heslop (1938). "*Argynnis selene*, a butterfly new to the Isle of Rhum." Entomologist, 71: 213.

Previously recorded from Soay and Skye.

45. Harrison, J. W. Heslop (1938). "The Rhopalocera of the islands of Rhum, Eigg, Muck, Eilean nan Each and Heisker (Inner Hebrides), and of Harris, North Uist, South Uist, Eriskay, Taransay and the Monach Islands (Outer Hebrides)." Entomologist, 71: 265–7.

Fourteen species of butterflies occur in these islands.

2. GENERAL REPORTS AND TAXONOMIC STUDIES OF USE TO ECOLOGISTS

See also Section 4

46. Jenkin, B. M. & Mortimer, C. H. (1938). "Sampling lake deposits." Nature, Lond. 142: 834–5.

Describes a new form of apparatus for taking samples of deposits from the bed of lakes etc. By means of rotating half-cylinders a core can be obtained from any depth, undistorted by compression, a disadvantage formerly associated with all forms of mud samplers.

47. **Deraniyagala, P. E. P.** (**1938**). "The loggerhead turtles in the National Museum of Ireland, with special reference to those taken in Irish waters." Irish Nat. J. 7: 66–70.

Systematic and distributional notes on the museum collection of Carettidae, including the recognition of Irish specimens of *Colpochelys kempi*, which is normally restricted to waters of the Gulf of Mexico.

48. **Burr, M.** (**1938**). "The Orthoptera of North Germany." Ent. Rec. 50: 146–8.

Comparison with the British fauna.

49. **China, W. E.** (**1938**). "Corrections and additions to James Edwards' catalogue of British Hemiptera-Homoptera, Perth, 1908 (excluding Psyllidae)." Ent. Mon. Mag. 74: 191–7.

An important revision of the list of British species and of their nomenclature.

50. **Thomas, D. C.** (**1938**). "An annotated list of species of Hemiptera-Heteroptera not hitherto recorded for Middlesex." Entomologist, 71: 148–53.

Records 88 new species, bringing the county total to 242, with notes on abundance, etc.

51. **China, W. E.** (**1938**). "Some Homoptera new to the British list." Ent. Mon. Mag. 74: 235–44.

Includes key to the British species of *Megamelus*.

52. **Smart, J.** (**1934**). "On the biology of the black fly, *Simulium ornatum* Mg." Proc. R. Phys. Soc. Edinb. 22: 217–38.

A full account, including the description of an apparatus for rearing Simuliidae.

53. **Goddard, W. H.** (**1938**). "The description of the puparia of fourteen British species of Sphaeroceridae (Borboridae, Diptera)." Trans. Soc. Brit. Ent. 5: 235–58.

These flies were bred on several different materials, including decaying lawn-mowings, garden refuse, and the dung of cows, deer, sheep and mice.

54. **Edwards, F. W.** (**1938**). "On the British Lestremiinae, with notes on exotic species. 5 [6, 7]. (Diptera, Cecidomyiidae.)" Proc. R. Ent. Soc. Lond. B, 7: 199–210, 229–43, 253–65.

55. **Rolfe, S. W.** (**1937**). "Notes on Diplopoda. IV. The recognition of some millipedes of economic importance." J. S.-E. Agric. Coll. Wye, 40: 99–107.

56. **Rolfe, S. W.** (**1938**). "Notes on Diplopoda. V. The recognition of some millipedes of economic importance. II." J. S.-E. Agric. Coll. Wye, 42: 214–15.

(**55** and **56**.) Recognition characters and habitat notes concerning four "flat-backed" millipedes, three belonging to the family Polydesmidae and one to the Strongylosomidae; and eight "snake" millipedes, five belonging to the Iulidae and three to the Blaniulidae.

57. Lebour, M. V. (1937). "The eggs and larvae of the British Prosobranchs with special reference to those living in the plankton." J. Mar. Biol. Ass. U.K. 22: 105–66.

A summary of present knowledge of the larvae of all British Prosobranch Mollusca, with descriptions of the eggs. Full bibliography.

3. ANIMAL BEHAVIOUR AND THE ACTION OF ENVIRONMENTAL FACTORS

See also **3, 4, 10, 15, 41, 105, 112, 139, 152, 154, 175, 185, 186, 188**

58. Laurie, R. Douglas & Jones, J. R. Erichsen (1938). "The faunistic recovery of a lead-polluted river in north Cardiganshire, Wales." J. Anim. Ecol. 7: 272–89.

After describing the way in which pollution occurred by the oxidation of lead sulphide to lead sulphate, records are presented of surveys, giving lists of animals and amounts of lead in the water, from 1921 (when the last mine stopped working and the fauna comprised only 14 species, mostly insects) to 1937. By 1932 the recovery, shown by a list of 103 species, had permitted enough trout for fishing, and now the river is considered practically normal.

59. Pentelow, F. T. K., Butcher, R. W. & Grindley, J. (1938). "An investigation of the effects of milk wastes on the Bristol Avon." Minist. Agric. Fish., Fish. Invest. Ser. 1, 4, No. 1: 1–76. (London: H.M. Stationery Office. Price 4*s*. 6*d*.)

Pollution is less severe at Chippenham from the dried and condensed milk products than where the effluent contains whey from butter or cheese making. Indicators of pollution were increased turbidity; presence of "sewage fungus" (*Sphaerotilus natans, Cladothrix dichotoma*) black silt, *Asellus* and leeches; and low dissolved oxygen content. The situation was improved by putting part of the wastes through the town sewers. Methods of chemical analysis are listed with authority. Algae were studied, in part, by the glass plate method; invertebrates were collected with Percival's scoop. Species given with notes on abundance.

60. Marshall, F. H. A. (1936). "Sexual periodicity and the causes which determine it." Philos. Trans. B, 226: 423–56.

A very good general review of the field of sexual periodicity, which will be of great use to physiologists and ecologists alike. (See Review in J. Anim. Ecol. (1939) 8: 173.)

61. Rowlands, I. W. (1938). "Preliminary note on the reproductive cycle of the red squirrel (*Sciurus vulgaris*)." Proc. Zool. Soc. Lond. A, 108: 441–3.

A preliminary investigation of 388 specimens suggests that the breeding season is prolonged, the peak in male activity being in December and January, while pregnant females were obtained nearly all the year round, though details are not yet enough to show a similar peak.

62. Brambell, F. W. R. & Rowlands, I. W. (1936). "Reproduction of the bank vole (*Evotomys glareolus*, Schreber). I. The oestrous cycle of the female." Philos. Trans. B, 226: 71–97.

The breeding season is from the middle of April until the beginning of October. It is estimated that one female may rear four or five litters in a season. The mean number of foetuses *in utero* in 70 late pregnancies was 4·11. Ovulation occurs spontaneously in the absence of copulation. There is a well-marked anoestrus with vaginal closure.

63. Rowlands, I. W. (1936). "Reproduction of the bank vole (*Evotomys glareolus*, Schreber). II. Seasonal changes in the reproductive organs of the male." Philos. Trans. B, 226: 99–120.

Seasonal activity of the male commences early in March. Young males born early in the breeding season become sexually mature before the end of the same season. In November there is complete cessation of spermatogenetic activity.

64. Deanesly, R. (1935). "The reproductive processes of various mammals. Part IX. Growth and reproduction in the stoat (*Mustela erminea*)." Philos. Trans. B, 225: 458–92.

The stoat has a restricted breeding season. The young are all born in early spring, generally in April, and lactation lasts about 5 weeks. They may come into oestrus and ovulate while still lactating, but no second pregnancies were found. The reproductive cycle is, therefore, of a type hitherto undescribed. The essentials are—short effective breeding season, although the female ovulates all the year round, and the occurrence of fertile males during two-thirds of the year. The limitation may be due to a seasonal change in the pituitary.

65. Baker, J. R. & Ranson, R. M. (1938). "The breeding seasons of Southern Hemisphere birds in the Northern Hemisphere." Proc. Zool. Soc. Lond. A, 108: 101–41.

Contains a complete summary of records dealing with this problem. Some species show a persistence of the native rhythm, others are modified by changed external factors.

66. Rowan, W. (1938). "London starlings and seasonal reproduction in birds." Proc. Zool. Soc. Lond. A, 108: 51–77.

Much of the theory based on recent physiological work upon migration is questioned, particularly that dealing with the effect of light intensity. Starlings from winter roosts on London buildings were found to have enlarged gonads, though the light reaching them was negligible. The factor responsible may have been wakefulness caused by traffic.

67. Lind, E. M. (1938). "Studies in the periodicity of the algae in Beauchief Ponds, Sheffield." J. Ecol. 26: 257–74.

Increase in algae in 1934–5 followed spawning of frogs, probably through increased phosphates (p. 262). Brief notes on animal life are given.

68. Raymond, C. J. (1938). "Brown-trout geology: a comparison of trout growths and geological strata." Salm. Trout Mag. No. 93: 329–38.

Data on the rate of growth of brown trout, based on scale-readings, from 14 different waters in Great Britain and an attempt to correlate the growth rate with the geology of the various districts. No chemical data are given.

69. Marshall, S. M., Nicholls, A. G. & Orr, A. P. (1937). "On the growth and feeding of the larval and post-larval stages of the Clyde herring." J. Mar. Biol. Ass. U.K. 22: 245–67.

This paper also contains an account of experiments on oxygen consumption and temperature toleration.

70. **Bull, H. O. (1938).** "Studies on conditioned responses in fishes. Part VIII. Discrimination of salinity changes by marine Teleosts." Rep. Dove Mar. Lab. No. 5: 19–35.

Carefully controlled experiments with 17 species show that these fish are able to perceive small salinity changes, such as occur naturally, and will respond purposively to them.

71. **Kozhantshikov, I. W. (1938).** "Physiological conditions of cold-hardiness in insects." Bull. Ent. Res. 29: 253–62.

Cold-hardiness depends on the physiological state of the organism, e.g. insects in diapause are more hardy than insects stopped in their development, while growing insects are practically non-cold-hardy. The difference in cold-hardiness in these groups depends on the specificity of their cellular respiration. The cellular respiration of cold-hardy insects is characterized by its definite thermostable part.

72. **Brown, S. C. S. (1938).** "Mortality amongst larvae of *Stenoptilia graphodactyla*, Treits. (Lep. Pyralidina). Ent. Rec. 50: 149.

Larvae of this plume moth entering closed flowers of *Gentiana pneumonanthe* are protected from the weather; occasionally they enter expanded flowers and are likely to be drowned in trapped rain-water.

73. **Morris, S. (1938).** "The life story of *Apatura iris*." Entomologist, 71: 156–60.

Conclusion of a detailed study of the life history of this butterfly.

74. **Williams, C. B. (1936).** "The influence of moonlight on the activity of certain nocturnal insects, particularly of the family Noctuidae, as indicated by a light trap." Philos. Trans. B, 226: 357–89.

75. **Russell, S. G. Castle (1938).** "The third brood of *Heodes* (*Lycaena*) *phlaeas*, Linn., 1761." Ent. Rec. 50: 1–2.

The author is not convinced that a third brood of this butterfly does occur in nature in this country in any appreciable numbers. See also **T. B. Fletcher** (1938). Ent. Rec. 50: 56.

76. **Querci, O. (1938).** "Influence of reflected radiations on insects." Ent. Rec. 50: 42–3.

Larvae of the large white butterfly were confined in boxes of white paper and exposed to radiations. Temperatures attained and length of life under these conditions are briefly indicated, also the effect of wind.

77. **Cockayne, E. A. (1938).** "Notes on the life-history of *Leucania l-album*, L." Ent. Rec. 50: 13–18.

A rare immigrant moth which apparently reached the south coasts in large numbers about 1933 and has continued to breed here.

78. **Tulloch, J. B. G. (1938).** "Early swarms of bees." Entomologist, 71: 197.

There was no rain or frost during February and March 1938 at Abergavenny. The author's bees began work about 14 February; a swarm emerged on 7 April to be followed by second and third swarms from the same hive on 14 and 17 April!

79. Guichard, K. M. (1938). "*Andrena humilis* and *Picris hieracioides*." Ent. Mon. Mag. 74: 233–4.

Andrenid bees are the primary fertilizing agents of the flowers of *Picris hieracioides*.

80. Blackburn, K. B. (1938). "Pollination of a rare Alpine plant by a Carabid beetle." Entomologist, 71: 238.

Carabus monilis observed in the Island of Rhum collecting at flowers of *Cherleria sedoides*.

81. Andrews, H. W. (1938). "Retarded emergence in Trypetidae." Ent. Rec. 50: 26–7.

Records emergence in 1937 of *Trypeta vectensis* and *Euribia spoliata* from seedheads gathered in 1935 which had already produced a batch of flies in 1936.

82. Thomson, R. C. Muirhead (1938). "The reactions of mosquitoes to temperature and humidity." Bull. Ent. Res. 29: 125–40.

The reactions of *Culex fatigans* to temperature studied by means of a new type of temperature gradient apparatus based on the same principle as the humidity alternative character. Its reactions to humidity were studied by means of the alternative chamber in a dark constant temperature room at 25° C.

83. Mellanby, K. (1938). "Diapause and metamorphosis of the blowfly, *Lucilia sericata* Meig." Parasitology, 30: 392–402.

Diapause is common in this species and is caused by overcrowding, dry meat, heat or desiccation which prevent the corpus allatum from secreting a necessary hormone. It is an advantageous arrangement by which pupation is prevented until the conditions are suitable for the more fragile adult.

84. Butler, G. C. (1938). "A further contribution to the ecology of *Aleurodes brassicae* Walk. (Hemiptera)." Proc. R. Ent. Soc. Lond. A, 13: 161–72.

Discusses parasites and predators, effects of high and low temperatures on survival and on oviposition, effect of humidity on oviposition, causes of migration and effect of various biotic and physical factors in nature.

85. Fletcher, T. B. (1938). "Early dates for grasshoppers." Ent. Rec. 50: 94.

Five species were adult unusually early in 1938 at Rodborough, Glos.

86. Harvey, L. A. (1938). "Preliminary note on the relations between grasshoppers and the recolonisation of denuded heath- and moor-land vegetation." Trans. Soc. Brit. Ent. 5: 291–7.

The distribution of several species of grasshopper has been determined in relation to burned and unburned ground in Devon. *Myrmeleotettix maculatus* occurs on the burned areas and is absent or very sparse on unburned ground. *Chorthippus parallelus* and *C. bicolor* are found in the thick vegetation of the unburned areas, and only colonize the burned ground heavily as the vegetation begins to recover and form a relatively dense cover.

87. **Fox, H. M., Wingfield, C. A. & Simmonds, B. G. (1937).** "The oxygen consumption of Ephemerid nymphs from flowing and from still waters in relation to the concentration of oxygen in the water." J. Exp. Biol. 14: 210–18.

There is an extreme contrast between *Cloëon dipterum* and *Baëtis* sp. in the relation between oxygen consumption and oxygen concentration in the water. A relation exists between oxygen consumption and size of animal, for instance, the oxygen consumption of the larger species *Leptophlebia marginata* is lower than that of the smaller species *L. vespertina*.

88. **Anon. (1938).** "The possibility of improving Scotch lochs." Game and Gun, 15: 328.

The acid lochs of Scotland are unsuitable for the common shrimp (*Gammarus pulex*), which, however, was believed to thrive in fresh water of Ireland. Samples of shrimp from lochs having a wide range of *p*H contained almost entirely *G. duebeni*, usually found in brackish water. Its possible importation as a food for Scotch trout is discussed.

89. **Thomas, H. Dighton (1937).** "Fossils and their original environment." S. East Nat. 42: 46–64.

A demonstration of the existence and action, in the palaeontological history of marine faunas, of exactly the same environmental control as is found in the study of living marine animals.

90. **Moore, Hilary B. (1937).** "A comparison of the biology of *Echinus esculentus* in different habitats. Part III." J. Mar. Biol. Ass. U.K. 21: 711–19.

Seasonal changes in gonad volume in sea urchins from Plymouth compared with those from Port Erin. The mean size of sea-urchins increases towards the south. Comparison is made between specimens from Millport, Port Erin, and Plymouth. The pigments present in sea-urchins appear to be derived from the food. A diagram is given of the seasons of shell and gonad growth, spawning, etc., at Plymouth.

91. **Moore, Hilary B. (1937).** "The biology of *Littorina littorea*. Part I. Growth of the shell and tissues, spawning, length of life and mortality." J. Mar. Biol. Ass. U.K. 21: 721–42.

92. **Wilson, D. P. (1937).** "The influence of the substratum on the metamorphosis of *Notomastus* larvae." J. Mar. Biol. Ass. U.K. 22: 227–43.

An account of experiments to show that the larvae of *Notomastus latericeus* Sars, a mud-dwelling Polychaete, exercise some choice of the soil on which they settle. It is pointed out that such choice, if general, would have important bearings on distribution problems.

93. **Graham, M. (1938).** "Phytoplankton and the herring. Part III. Distribution of phosphate in 1934–1936." Minist. Agric. Fish., Fish. Invest. Ser. 2, 16, No. 3: 1–26. (London: H.M. Stationery Office. Price 2*s*.)

Includes 15 charts of horizontal and vertical stratification of phosphate in the North Sea. Success of *Rhizosolenia* (which may interfere with herring fishing) is influenced not only by a strong Atlantic influx of nutrient salts, but probably by a complex of factors associated with the influx.

94. Jenkin, P. M. (1937). "Oxygen production by the diatom *Coscinodiscus excentricus* Ehr. in relation to submarine illumination in the English Channel." J. Mar. Biol. Ass. U.K. 22: 301–43.

A full account of experiments on the relation of photosynthesis to energy in the sea. The cultures of diatoms were exposed to light at various depths. A method is described for calculating the available energy at any depth in Joules or g. cals.

95. Atkins, W. R. G. & others (1938). "Measurement of submarine daylight." J. Cons. Int. Explor. Mer, 13: 37–57.

In this report of an international committee suggestions are made of a standard method for the measurement of light intensity by a photoelectric cell. Errors and necessary corrections are discussed and practical advice given for the construction of apparatus and its use at sea. An electrical transparency meter is also described.

96. Fox, H. M. & Wingfield, C. A. (1938). "A portable apparatus for the determination of oxygen dissolved in a small volume of water." J. Exp. Biol. 15: 437–45.

Only 1–2 c.c. of water are required for the estimation, and the method is accurate to 2%.

97. Gunn, D. L. & Kennedy, J. S. (1936). "Apparatus for investigating the reactions of land Arthropods to humidity." J. Exp. Biol. 13: 450–9.

4. PARASITES

See also **84, 128, 153**

98. Mayfield, R. B. (1938). "Rat-fleas in Plymouth." Parasitology, 30: 314–19.

Seventy-seven rats (*Rattus norvegicus* and *R. rattus*) were trapped in an isolated part of the docks and six in the town. On both groups the fleas *Nosopsyllus fasciatus* and *Leptopsylla segnis* were found, and in the dock group *Xenopsylla cheopis* was common. The collection was made over three years and seasonal variations are discussed though the data are admittedly scanty.

99. Buxton, P. A. (1938). "Studies on populations of head-lice (*Pediculus humanis capitis*: Anoplura). II." Parasitology, 30: 85–110.

Using 2000 hair crops collected from Africa, Ceylon and Palestine, detailed data have been obtained on the relation of the head lice count to the race, sex, age and weight of hair of the host individual and to the season of the year. As these relationships may be bound up with local or racial customs the investigations could be extended most profitably by people who are well acquainted with the localities.

100. Leiper, J. W. G. & Clapham, P. A. (1938). "Some Nematode parasites found in Chinese water deer (*Hydropotes inermis*), with a description of *Trichostrongylus cevarius* n.sp." J. Helminth. 16: 77–82.

Viscera of 24 water deer bred in Whipsnade Park were examined and 14 species of Nematode newly recorded. All except three of these are such as are common to the district. A new species, and two species of *Ostertagia* (*O. lyrata* and *O. gruhneri*) have not been recorded in England before. Probably these are natural parasites of the deer in China and came over with the original stock.

101. Clapham, P. A. (1938). "New records of helminths in British birds." J. Helminth. 16: 47–8.

These records show that the host range of many helminth species is considerably wider than had been suspected.

102. Clapham, P. A. (1938). "Are there host strains within the species of *Syngamus trachea*?" J. Helminth. 16: 49–52.

The view that physiological strains of the gapeworm become so adapted to one species of host that they cannot infect another is discounted by experiments in which this parasite has been transmitted to chickens and pheasants from rook, crow, jackdaw, magpie, jay, starling, and turkey strains. The infection was not direct, but via earthworms as intermediate hosts. Larvae remain infective in earthworms for up to 3½ years and this is probably the normal method of transmission of the disease.

103. Davies, T. I. (1938). "A description of *Hymenolepis neoarctica* n.nom., syn. *H. fusus* Linton, 1927, with a discussion on the synonymy of *Taenia fusus* Krabbe, 1869." Parasitology, 30: 339–43.

Strobilae of *H. neoarctica* and *H. ductilis* were found in the intestine of a greater black-backed gull (*Larus marinus*) shot near Aberystwyth. This is the first record for these species in the Old World and presents evidence of a Neoarctic element in the Cestode fauna of British gulls.

104. Thompson, G. B. (1938). "The parasites of British birds and mammals. XXI. Additions and corrections to previous contributions." Ent. Mon. Mag. 74: 277–9.

Forty-seven British species of fleas are now known.

105. Thompson, G. B. (1938). The parasites of British birds and mammals. XX. The ectoparasites of the house-martin, swift, swallow and sand-martin." Ent. Mon. Mag. 74: 147–51.

Nine species of biting lice have been recorded from these four birds, but only four are found frequently. The sand martin possesses a flea specific to itself, the house martin four specific species; the swallow and swift are almost free. The house martin is the only species parasitized by *Oeciacus hirundinis*, resembling a "bed-bug". In the British Isles the house martin and swift are parasitized by two species of Hippoboscid flies.

106. Davies, T. I. (1938). "Some factors governing the incidence of Helminth parasites in the domestic duck." Welsh J. Agric. 14: 280–7.

The nature of the geological information is responsible for determining the type of the prevalent species of parasite, e.g. flukes, are present in areas where the supply of natural lime allows a large population of fresh-water snails, but are absent where the surface waters are lime deficient. Rapid flowing streams dispose of helminth eggs and hinder the increase of colonies of the invertebrate secondary hosts.

107. Williams, G. (1938). "On the occurrence of *Scopelocheirus hopei* and *Cirolana borealis* in living *Acanthias vulgaris* (spiny dogfish)." Irish Nat. J. 7: 89–91.

The Amphipod parasite, *S. hopei*, was found in a number of living dogfish, destroying vulnerable soft tissues such as the gills, eye muscles and associated nerves. The optic nerves in each case remained uninjured. From 4 to 12 specimens were taken from each host. The occurrence of the Isopod *C. borealis* in Irish waters both as a free-living form and as a parasite on the dogfish is also recorded.

108. Baylis, H. A. (1938). "On two species of the Trematode genus *Didymozoon* from the mackerel." J. Mar. Biol. Ass. U.K. 22: 485–92.

The author gives reasons for dividing the former species *D. scombri* into two species, *scombri* and *faciale*. The first is found in cysts in the roof of the pharynx of the mackerel, the second behind the eye. A full description of *D. faciale* is given.

109. Christison, M. H., Mackenzie, I. & Mackie, T. J. (1938). "*Bacillus salmonicida* bacteriophage: with particular reference to its occurrence in water and the question of its application in controlling *B. salmonicida* infection. A report to the Fishery Board for Scotland." Fisheries, Scotland, Salmon Fish., 1938, No. 5: 1–18. (Edinburgh: H.M. Stationery Office. Price 1*s*.)

This phage may occur in winter or summer in waters infected or uninfected with furunculosis, and does not always occur in infected waters. It is widespread and of no value as an indicator of the disease. It had no inhibitory action on the course of epizootics among brown trout in tanks. Bacteriological technique fully described.

110. Salt, G. (1938). "Experimental studies in insect parasitism. VI. Host suitability." Bull. Ent. Res. 29: 223–46.

Host may be found and accepted, but not suitable because the attack is frustrated (i.e. host unsuitable for adult parasitoid) by host escaping attack; by host resisting actively or passively; and by host inhibiting oviposition. The parasitism may also be unsuccessful (i.e. host unsuitable for developing parasitoid) because host is physically unsuitable, e.g. in size, in texture, etc.; or because host is chemically unsuitable either as an environment or as food; or because host is biologically unsuitable, e.g. host dies, moves, moults, etc.

111. Bisset, G. A. (1938). "Larvae and pupae of Tachinids parasitizing *Pieris rapae* and *P. brassicae* L." Parasitology, 30: 111–22.

Larvae and pupae of these two species of *Pieris* were found to contain *Phryxe vulgaris*, *P. nemea*, *Epicampocera succincta*, *Compsilura concinnata*, and an unknown species which is described.

112. Cameron, E. (1938). "A study of the natural control of the pea moth, *Cydia nigricana*, Steph." Bull. Ent. Res. 29: 277–313.

Includes a comprehensive account of three parasites: *Ascogaster quadridentatus* (Braconid), *Glypta haesitator* (Ichneumonid) and *Angitia* sp. (Ichneumonid). The apparent significance of rainfall, sunshine and temperature on the moth's distribution in England is discussed.

113. Nixon, G. E. J. (1938). "A preliminary revision of the British Proctotrupinae (Hym., Proctotrupoidea)." Trans. R. Ent. Soc. Lond. 87: 431–66.

A study of an important group of parasitic Hymenoptera. Includes keys, many figures, distributional and host records.

114. Cole, H. A. (1938). "On some larval Trematode parasites of the mussel (*Mytilus edulis*) and the cockle (*Cardium edule*). Part II." Parasitology, 30: 40–3.

Describes a new cercaria *C. cambrensis* which infects all cockles collected from the Menai Straits. Its structure is very like that of a metacercaria found by Jameson in the mantle of mussels and thought to give rise to the pearl-inducing Trematodes. It may be an earlier stage of the same form. The pearl-inducing Trematode is common in mussels collected in this same locality.

5. FOOD AND FOOD-HABITS

See also **6**, **10**, **17**, **26**, **27**, **31**, **34**, **36**, **39**, **69**, **84**, **88**, **130**, **134**, **147**, **151**, **155**, **157**, **158**

115. Austin, M. D. & Rolfe, S. W. (1938). "The grey squirrel: a review of the present situation." J. S.-E. Agric. Coll. Wye, 42: 93–8.

A review article which includes a tabulated list showing the wide range of food consumed.

116. Elmhirst, R. (1938). "Food of the otter in the marine littoral zone." Scot. Nat.: 99–102.

The presence of otters on the shore is indicated by defaecation mounds often surrounded by bright green vegetation and used for generations. Remains of mammals, birds, fish, Crustacea (eight species) and rarely molluscs, have been found in the faeces and in places frequented. There are notes on habits of otters and the type of shore frequented by them.

117. Ford, J., Chitty, H. & Middleton, A. D. (1938). "The food of partridge chicks (*Perdix perdix*) in Great Britain." J. Anim. Ecol. 7: 251–65.

Crops of 69 chicks, mostly from hay, lucerne, etc., not from grain fields, showed that animal food predominates in the first two weeks, decreases by half at the end of the third week, and gives way to almost entirely plant food after three weeks.

118. Carpenter, G. D. H. (1937). "Bird as enemies of butterflies." S. East Nat. 42: 93–5.

A statement of the importance to the theory of mimicry of the question whether birds do or do not eat butterflies, and an invitation to amateur naturalists to co-operate in the work of answering it.

119. Anon. (1937). "Garden birds." J. Minist. Agric. 43: 1026–8.

Food habits of blackbird, song thrush, robin, dunnock (hedge sparrow) and wren.

120. Chitty, D. (1938). "A laboratory study of pellet formation in the short-eared owl (*Asio flammeus*)." Proc. Zool. Soc. Lond. A, 108: 267–87.

Experiments show that a fairly constant relationship exists between the time for pellet formation and the amount of the meal. Quantitative data on food consumed suggest that about $2000 \pm 50\%$ voles (*Microtus*) may be taken in a year. In an area on the Scottish border in April 1933, when a vole census was done concurrently with one of short-eared owls, the toll would represent 0·02 to 0·05% of the population daily.

121. Anon. (1937). "Interesting birds: (1) The barn owl." J. Minist. Agric. 43: 1124–5.

Remarks on food habits. Further references in J. Minist. Agric. 44: 6 (nightjar), 108–9 (kestrel), 204 (blackbird), 310–11 (song-thrush), 421 (robin), 519 (wren), 612–13 (long-tailed tit), 722–3 (spotted flycatcher), 830 (lapwing).

122. Deane, C. Douglas (1938). "Observations on the rook." Bird Notes and News, 18: 17–19.

There is a brief mention of pellet-casting in this species. In the neighbourhood concerned (Co. Down) they consisted mostly of grain with pieces of turnip and potato. At one nest they consisted almost entirely of burying beetles.

123. Glegg, W. (1938). "Birds taking rubber articles." Essex Nat. 26: 26–9.

A résumé of previous evidence on this subject is given together with new observations. Rooks, terns, gulls, starlings, puffins, and possibly carrion crows are involved. No significant choice of colour is noticed. The articles may be mistaken for food or swallowed to aid digestion.

124. Embry, B. (1938). "Isle of Wight and the seven toads: a sugaring experience. Entomologist, 71: 274.

Toads attacking moths attracted to sugar.

125. Neill, R. M. (1938). "The food and feeding of the brown trout (*Salmo trutta* L.) in relation to the organic environment." Trans. Roy. Soc. Edinb. 59: 481–520.

A study carried out on the river Don, in Aberdeenshire. The author comes to the following conclusions: (1) trout feed on the whole range of animals present, (2) the choice of food is governed by accessibility only, and hence, (3) the *quality* of food is not a limiting factor in the distribution of the brown trout. Lists are given of the flora and fauna of the region under observation.

126. Tchernavin, V. (1938). "The absorption of bones in the skull of salmon during their migration to rivers." Fisheries, Scotland, Salmon Fish. 1938, No. 6: 1–4. (Edinburgh: H.M. Stationery Office. Price 6*d*.)

The main bones of the jaw, palatines, vomer and supra-ethmoid increase their size at the expense of calcium from bones forming the gill-covers, the branchiostegals and postorbitals as well as from the scales. In fact jawbones and teeth, useless to a fasting fish, grow at the expense of certain essential bones.

127. Whitney, R. J. (1938). "A plague of the beetle *Harpalus rufipes* Degeer." Ent. Mon. Mag. 74: 200–1.

"The beetles have evidently become conspicuous because, owing to the disturbance of their normal food supply, they now collect near the houses from the barren fields. How far this is related to the recent discontinuance of potato crops in the vicinity, it is not possible to say."

128. Murray, J. (1938). "The red spider and its prey." Northw. Nat. 13: 28.

The scarlet mite, *Anystis baccarum*, was twice noticed to attack a thrips (*Physothrips vulgatissimus*) and a moth fly (*Psychodes* sp.). Its presence in henhouses may be beneficial if it feeds on the various insect parasites of the birds.

129. Moore, H. B. (1938). "Algal production and the food requirements of a limpet." Proc. Malacol. Soc. Lond. 23: 117–18.

A study of limpets (*Patella vulgata*) living on an alga-covered wall. The areas eaten are plotted against the volumes of the limpets responsible, and show an approximately linear relationship.

6. POPULATIONS

See also **35, 39, 40, 41, 60–6, 83, 90, 91, 93, 99, 108, 110, 120, 169, 177, 184–8**

130. Fenton, E. Wyllie (1938). "Biological notes for 1937." Scot. J. Agric. 21: 74–81.

A remarkable increase of rabbits in 1937; badgers also increasing in numbers and in extent of range. Blackbirds in the dry summer changed from their habits of turning over dead leaves and material on the ground to uprooting plants in order to get grubs. The younger generation learned this new habit and kept to it. Mass movements and temporary increase in numbers of the antler moth causing special damage to moor mat grass (*Nardus stricta*) and the rushes (*Juncus squarrosus*).

131. Anon. (1938). "The stock-carrying capacity of hill grazings in Scotland—I–II." Scot. J. Agric. 21: 219–32, 345–63.

The decline in sheep stocks in the Highland counties has been largely due to the establishment of deer forests. Other factors involved are bracken, unbalanced grazing by sheep, heather, drainage and removal of lime and phosphates, etc., and damage by rabbits and mountain hares. Figures of the numbers of sheep in Argyll, Inverness, Perth, Ross and Cromarty and Sutherland since 1855 to date are given.

132. Middleton, A. D. (1937). "Whipsnade Ecological Survey, 1936–7." Proc. Zool. Soc. Lond. A, 107: 471–81.

A preliminary survey of the animals living in a wild or semi-wild state at Whipsnade including population counts. Since 1933 wallabies (*Macropus*) have remained stationary. Chinese water deer (*Hydropotes inermis*) have fluctuated greatly and have been reduced once by an epidemic, while muntjac deer (*Muntiacus muntjac*) have remained at the initial level. Some figures are also given for rabbits, rats, squirrels and continental dormice (*Glis*).

133. Matheson, C. (1938). "Weights of brown and black rats." Naturalist, Lond. No. 980: 251–3.

Weight distribution of brown rats from the official rat-catching returns of Cardiff. Fewer data are available for the black rat. In both species information is needed on the sex ratio.

134. Moon, J. H. (1938). "Mortality among mute swans on Ullswater." Northw. Nat. 13: 25.

Every swan that takes up its abode on Ullswater dies. During the past three years thirteen swans which have died in this way have been examined. The food contents were unidentifiable but in every case lead was found in the tissues. Some food plant may be responsible both in this case and in that of the mortality of whooper swans on Loch Dochart. A. A. Dallman suggests *Lobelia dortmanna* as a possible cause.

135. Huxley, J. S. (1938). "Nests and broods in Whipsnade sanctuary in two successive years." Proc. Zool. Soc. Lond. A, 108: 445–52.

A number of tables and figures show how the year 1937, being less favourable than its predecessor, exerted an effect upon total nests, nests occupied, the number in which hatching took place, the size of clutch, the number of young hatched and the number of young fledged.

136. Fisher, J., Stewart, M. & Venables, L. S. V. (1938). "Gannet colonies of Shetland." Brit. Birds, 32: 162–9.

A description, census (2045 pairs) and history of the Hermaness colony.

137. Vevers, H. G. & Fisher, J. (1938). "The 1938 census of gannets (*Sula bassana*) on Ailsa Crag." J. Anim. Ecol. 7: 303–4.

On some parts there has been an increase, on others a decrease, with a net over-all decrease of 9·4% since 1937.

138. Fisher, J. & Venables, L. S. V. (1938). "Gannets (*Sula bassana*) on Noss, Shetland, with an analysis of the rate of increase of this species." J. Anim. Ecol. 7: 305–13.

The colony is described, and relations with other birds noted. The analysis, made after consultation with J. B. S. Haldane and C. F. Fisher, is presented with a graph of the theoretical and actual increase. It shows that the increase from one pair in 1914 to 1518 pairs in 1938 is due to colonization as well as to breeding up to certainly 1935.

139. Kemp, S. (1938). "Oceanography and the fluctuations in the abundance of marine animals." Nature, Lond. 142: 777–9 and 817–20.

The annual, restricted, fluctuations are masked by long-term fluctuations. At Plymouth there has been a decline in the numbers of young fishes since 1931, correlated with a decrease in phosphate in the water, apparently due to change in water movements off the Atlantic mouth of the Channel, leading to a shortage of mixed Atlantic ("*elegans*") water. There is no correlation of these phenomena with temperature or salinity observations in the Channel, but there is evidence of long-term fluctuations from Norway and from West Greenland, which are apparently due to changes in temperature. The author calls attention to the need for a fuller hydrographic investigation of the eastern Atlantic, and to the fact that, with certain exceptions, the scientific administration of fisheries in the British Empire is either deficient or lacking.

140. Farran, G. P. (1937). "The herring fisheries off the north coast of Donegal." J. Dep. Agric. Saorstát Éireann [Éire], 34: 262–70.

Summary of the Department's work from 1921–35. Explanation of the use of population analysis for forecasting a season's catch. Unfortunately, the life history is not known before herring join the shoal (usually at 3–4 years). Maximum age reached is 12 years.

141. Farran, G. P. (1938). "On the size and number of the ova of Irish herrings." J. Cons. Int. Explor. Mer, 13: 91–100.

Distinction between spring and autumn spawners from size of ova in relation to weight of gonad.

142. Hickling, C. F. (1938). "The English plaice-marking experiments 1929–32." Minist. Agric. Fish., Fish Invest. (1937), Ser. 2, 16, No. 1: 1–80. (London: H.M. Stationery Office. Price 4*s*.)

19,684 plaice were marked between 1929 32 and 6750 were recaptured, five in the sixth year after release. There is a rough general rate of decrease of 70% per annum. Distribution from marking stations off the Dutch, German and Danish coasts is shown on maps. A useful system of weighted contouring is used to make allowance for the seasonal difference in chance of recapture by fishing vessels. Considerable mixing of stocks has occurred, being at its greatest after one year. In winter, while English steam trawlers make wide cruises, the contribution of fish recaptured by other nationalities is small and largely from the coast. Since the faster growing plaice move offshore their inclusion in greater numbers in the spring and summer samples affects to an unknown extent the graph showing growth rate: which, however, does seem to be greatest just then. Returns of the smallest sizes are least frequent probably because they are not marketable and are thrown back. There is some evidence that the fishing practice of Denmark with short period seine hauls may prevent excessive deaths among these rejected fish.

143. Robertson, J. A. (1938). "The sprat and the sprat fishery of England." Minist. Agric. Fish., Fish Invest. Ser. 2, 16, No. 2: 1–100. (London: H.M. Stationery Office. Price 4*s*. 6*d*.)

Sprat fishing is carried out on a small, local scale from lightly equipped boats operating in territorial waters. The number of localities engaged in the trade is only a small part of those that might be developed. There is considerable fluctuation in the landings, particularly in Norway, much less in Britain; but there is no general correspondence between different countries. Norway has a virtual monopoly of the imports, which have fetched £6. 13*s*. per cwt. compared with only 3 to 16*s*. paid for British landings. The British canning industry might profitably be expanded; but as the sprat is taken as a winter immigrant the seasonal nature of the trade is an objection. Statistics of age-composition and length-frequency from scale analysis are given, without any summary. The English and Norwegian fisheries depend chiefly on immature yearlings, which, though of the same year class, are taken younger in Norway as the season opens in May. Copepods are the main food. Technique of fat extraction is given: the yield is good (14–20%) at the season's start, dropping to 5–7% at the end. Parasites were *Lernaeenicus sprattae* on 46 out of 62 fish, *L. encrasicola* on 15, both species on one only (though the former sticks on the eye, the latter on the body).

144. Russell, F. S. (1937). "The seasonal abundance of the pelagic young of Teleostean fishes in the Plymouth area. Part IV. The year 1936, with notes on the conditions as shown by the occurrence of plankton indicators." J. Mar. Biol. Ass. U.K. 21: 679–96.

Russell, F. S. (1938). "On the seasonal abundance of young fish. V. The year 1937." J. Mar. Biol. Ass. U.K. 22: 493–500.

A comparison with the reports of previous years (1930–5). In both 1936 and 1937 there were very small numbers of *Sagitta elegans*, and, correlated with this, there was a complete absence of the usual peak of young spring spawners.

145. Graham, M. (1938). "Rates of fishing and natural mortality from the data of marking experiments." J. Cons. Int. Explor. Mer., 13: 76–90.

A simplified mathematical discussion of the planning and use of marking experiments on fish.

146. Éire, Dep. Agric., Fish. Branch [1938]. "Statistics of salmon, sea trout and eels captured during each of the years 1937, 1935, 1933, 1931, 1929, 1927." Pp. 1–19. (Government Publications Sale Office, 3–4 College St., Dublin. Price 4*d*.)

Tables without discussion.

147. Macfarlane, P. R. C. (1938). "Salmon of the upper Solway district 1934." Fisheries, Scotland, Salmon Fish. 1938, No. 3: 1–18. (Edinburgh: H.M. Stationery Office. Price 1*s*.)

Examination of 1890 sets of scales from nets set near the mouth of the River Annan showed that the fishery depends chiefly on grilse and small summer fish (79%). Previously spawned fish (1·1%) were in the lowest proportions yet found. 88% of the smolts had migrated when two-years old, thus giving a low average age, as expected from the low latitude. The calculated lengths of smolts were equal to the highest previously found (River Nith). Of the three neighbouring rivers, Annan, Nith and Dee, feeding conditions are inferior in the latter. This probably accounts for the smaller average length and higher average age at migration observed in the Dee smolts.

148. Hartley, G. W. (1938). "Salmon caught in the sea—West Sutherland, 1937." Fisheries, Scotland, Salmon Fish. 1938, No. 2: 1–21. (Edinburgh: H.M. Stationery Office. Price 1*s*. 3*d*.)

Grilse formed 72% of the catch; spring fish 13% (only 2·5% in 1936 and unusually plentiful for a west coast fishery); small summer fish 12%; previously spawned fish less than 2% (unusually scarce). Smolt ages were: 2-year 64%; 3-year 34%. Condition of the three-year-old smolts was generally better than that of the two-year-old, a reversal of 1936 conditions.

149. Hutton, J. A. (1938). "Wye salmon. Results of scale-reading, 1937." Salm. Trout Mag. No. 90: 49–72.

Statistics of the number, weight and age of salmon caught by rods and nets in the River Wye in 1937. The total catch was 3568 fish weighing 62,661½ lb. Scales of 991 fish were examined for age determination. All classes were present, but large springers, i.e. those which had spent three years in the sea, predominated. Graphs showing the annual variations in catch since 1905 are included.

150. Nall, G. H. & Macfarlane, P. R. C. (1938). "Sea trout of the river Carron and Loch Doule (Dhughaill), Western Ross-shire; with an appendix on Salmon from the same river." Fisheries, Scotland, Salmon Fish. 1938, No. 4: 1–42. (Edinburgh: H.M. Stationery Office. Price 2*s.* 6*d.*)

1811 sets of scales were obtained from captures by rod and for marking work. Percentage migrating after two, three and four years of parr life and lengths of smolts at migration were: 2-year 26%, av. 16·5 cm.; 3-year 63%, av. 18·7 cm.; 4-year 10%, av. 21·3 cm. In the first winter after migration (i.e. as whitling) only 2% spawned; in the second winter 61%; in the third 34%. Sea trout, unlike salmon, seldom fail to spawn in successive years. One fish had 11 spawning marks. Carron sea trout stand high among the slower growing Scottish types which the physiography of the west coast tends to produce.

151. Allen, K. R. (1938). "Some observations on the biology of the trout (*Salmo trutta*) in Windermere." J. Anim. Ecol. 7: 333–49.

Trout caught in a seine net from the upper three metres along the shore at all seasons from November 1933 to October 1935 furnish the basis for a detailed study of growth, the age at which trout enter the lake, their condition, their food at different seasons, and an estimate of the total numbers, by ages, in the littoral region.

152. Allen, K. R. (1938). "Deterioration of Windermere trout. An attempt at an explanation." Salm. Trout Mag. No. 91: 152–6.

From a consideration of the numbers, ages, growth and mortality rates, the food and predators of the present stock of trout in Windermere it is concluded that the alleged deterioration of the trout fishery during the last 30 years cannot be ascribed to unfavourable conditions in the lake. It is suggested that the cause must be sought in the streams to which the fish go to spawn and where they spend the first year or two of their lives.

153. Laing, J. (1938). "Host-finding by insect parasites. II. The chance of *Trichogramma evanescens* finding its hosts." J. Exp. Biol. 15: 281–302.

The rate at which the parasite found the host eggs varied inversely with its distance from them.

154. Ford, J. (1938). "Fluctuations in natural populations of Collembola and Acarina. Part 2." J. Anim. Ecol. 7: 350–69.

An analysis of the way in which the numbers of very small animals in a small habitat (a small ecosystem) fluctuate in relation to environmental changes and other causes. The age distribution of the spring-tail (*Pseudachorutes subcrassus*) was analysed during increase and decrease in numbers, and the variation in its distribution throughout the habitat was compared with fluctuations in numbers.

155. Meikle, A. A. & Macfarlan, J. (1938). "Damage to pasture by the larvae of the bracken-clock." Scot. J. Agric. 21: 183–5.

Larvae of *Phyllopertha horticola* at a density of nearly 435,000 to the acre completely destroyed the turf over two acres. Birds had added to the damage by tearing up the turf.

156. Roebuck, A. (1938). "Beetles in a church." Ent. Mon. Mag. 74: 209.

Includes average daily counts of *Xestobium rufo-villosum* (death-watch beetle) for various periods between 6 April and 8 June 1938.

157. Cameron, A. E. (1938). "The antler moth on Scottish hill-pastures." Scot. Nat.: 125–7.

Infestations are confined to hill pastures, and the first indications are often given by the presence of flocks of insectivorous birds attracted by the larvae. The final ecdysis is followed by mass migration of larvae, rarely down hill, in which many are drowned in hill streams and drains. This checks the infestation. Experimental investigations indicate that many of the surviving larvae are destroyed by bacterial disease.

158. Pickles, W. (1938). "Populations, territories and biomasses of ants at Thornhill, Yorkshire, in 1937." J. Anim. Ecol. 7: 370–80.

This is the third year of the survey of ants' nests on the same area to determine the increase or decrease of nests, of ants, by number and also by live weight (biomass), and population densities. The surveys for 1935 and 1936 were described in J. Anim. Ecol. (1936) 5: 262–70, and (1937) 6: 54–61, respectively.

159. Donisthorpe, H. (1938). "Observations on a colony of *Acanthomyops* (*Dendrolasius*) *fuliginosus*, Latr., for 23 years." Ent. Rec. 50: 73–6.

The establishment of this colony was observed in 1915, since when 45 named species of myrmecophiles have been found in it.

160. Morley, B. D. W. (1938). "Some observations on a mixed *Acanthomyops* (*Dendrolasius*) *fuliginosus*, Latr., *Acanthomyops* (*Chtonolasius*) *mixtus*, Nyl., colony." Ent. Rec. 50: 94–5.

Brief account of relations between these two species of ants. The belief is expressed that the *A. mixtus* element will die out since their numbers are relatively so few.

161. Boycott, A. E. & Oldham, C. (1938). "A contagious disease of *Helix aspersa*." Proc. Malacol. Soc. Lond. 23: 92–6.

Breeding experiments on individuals infected with a disease producing greying and wrinkling of the shell.

162. Russell, F. S. (1938). "The Plymouth offshore medusa fauna." J. Mar. Biol. Ass. U.K. 22: 411–39.

An account of the fluctuations in numbers and ratios of species of medusae obtained from weekly plankton hauls during the years 1930–7, together with ecological and morphological notes on certain species. The possibility of using some of the species as indicators is discussed.

163. Hardy, A. C. (1938). "Estimating numbers without counting." Nature, Lond. 142: 255–6.

Describes a method of estimating the number of organisms where only one or two species are present by visual comparison of the sample with a specially prepared chart. Very rapid estimations can be made with an accuracy of $\pm 15\%$.

164. Lowndes, A. G. (1938). "The density of some living aquatic organisms." Proc. Linn. Soc. Lond. 62–73.

An accurate method of determining the density of living aquatic organisms is described.

7. MIGRATION, DISPERSAL, AND INTRODUCTIONS

See also **16, 35, 47, 70, 77, 84, 93, 100, 115, 127, 130, 142, 145, 150, 151, 157, 186**

165. Robinson, H. W. (1938). "Recovery of ringed puffins in Orkney where marked." Scot. Nat.: 150.

Special rings are used, the overlapping kind being useless against the birds' beaks. Owing to a scarcity of these rings, preference in ringing was given to previously marked birds, of which 28 were recaptured.

166. Hendy, E. W. (1937). "Spring migration of swallows in south-west England." Discovery, 18: 336–8.

Observations on the spring migration routes of swallows made during the years 1934–7 by observers of the Bird-watching and Preservation Societies of Devon and Cornwall. The results favour the idea of definite routes rather than broad-front migration.

167. Green, J. T. & Flintoff, R. J. (1938). "Rookeries and roosts, and the desertion of rookeries. An ecological study." Northw. Nat. 13: 148–56.

In 1928 two large rookeries in Yorkshire were suddenly deserted in the middle of the breeding season though everything remained normal in other closely located rookeries. Carrion crows can hardly be held responsible for this desertion, as notes on the rookeries kept during the subsequent ten years show that crows, though common visitors, do not drive the rooks from their nests.

168. Russell, E. S. (1937). "Fish migrations." Biol. Rev. 12: 320–37.

Migrations usually involve a movement of mature fishes upcurrent to breed, followed by a dispersion of the spent fishes downcurrent which may develop into a definite feeding migration. The whole cycle tends to keep the species in its ecological norm. Marking experiments on cod, plaice and salmon are reviewed, with maps to illustrate these principles.

169. Ford, E. (1938). "Progress in fisheries research." Sci. Progr. 33: 63–5.

Brief review of (1) transplantation of fish species to new habitats, (2) the artificial propagation of plaice-flounder hybrids in Norwegian waters, (3) data on the growth rate of lobsters, and (4) data on variation in brood size from year to year in mackerel.

170. Menzies, W. J. M. (1938). "The movements of salmon marked in the sea. III. The island of Soay and Ardnamurchan in 1938." Fisheries, Scotland, Salmon Fish., 1938, No. 7: 1–9. (Edinburgh: H.M. Stationery Office. Price 1*s.* 3*d.*)

On the south shore of Skye 94 salmon were marked and released. Of the 22 recaptures 18 were on the north and east coasts of Scotland, only four on the west. Times of arrival fell into two groups on the east coast suggesting alternative routes east and west of the Outer Hebrides. Fish marked 25 miles farther south were recaught much more locally. However, of the 35 grilse (mostly) retaken out of 280 marked, three turned up in Ireland, one in Wales. This suggests that the station was on the fringe of the migration route passing south of the Outer Hebrides to the Irish, Welsh and west of England rivers.

171. "Piscator Senior" (1938). "Migrations of European salmon: results of Scottish and Norwegian markings." Salm. Trout Mag. No. 93: 288–99.

A useful popular account of the migrations of European salmon in the sea, based on the results of marking experiments carried out by the Scottish Fishery Board and by Knut Dahl in Norway. The conclusion is reached that the feeding grounds of the salmon are situated some distance to the west of the British Isles.

172. Calderwood, W. L. (1938). "Salmon towers. A new type of salmon pass in the Doon district." Salm. Trout Mag. No. 90: 29–36.

An unusual structure to enable salmon to surmount a dam, of unstated height, on the river Doon, Ayrshire.

173. Hardy, A. C. & Milne, P. S. (1938). "Studies in the distribution of insects by aerial currents. Experiments in aerial tow-netting from kites." J. Anim. Ecol. 7: 199–229.

An application of the marine plankton net to the collection of insects between 150 and 1945 ft. above the ground, mostly at Hull. The net, attached to a kite line, was opened and closed by an arrangement of strings released by the action of acid on copper wire, the time being controlled by the strength of the acid. Meteorological observations are given, and lists of the numerous insects collected at each height.

174. Grant, K. J. (1936). "The collection and analysis of records of migrating insects, British Isles, 1931–1935." Entomologist, 69: 125–31.

175. Wiltshire, E. P. (1938). "Notes on the winter flight, in mild climates, of vernal and autumnal moths." Ent. Rec. 50: 144–6.

Compares behaviour in England and Central Europe (cold winter, short summer); Taurus, Inner Syria, Kurdistan, etc. (cold winter, long summer); coasts of Cyprus, Syria and Palestine (mild winter, long summer).

176. Nicholson, C. (1938). "Further notes on *Danaus plexippus* L. in the British Isles." Entomologist, 71: 217–25.

Records 30 new appearances of this immigrant butterfly since 1935. Further reference in **E. Bolton King,** Entomologist, 71: 236.

177. Walker, J. J. (1938). "The comma butterfly, *Polygonia c-album* (Linn.): its decadence and revival as a British insect." Trans. Soc. Brit. Ent. 5: 281–90.

A summary of its occurrences during the long period of its eclipse over the greater part of its range in old times—omitting the records from Wales and the western English counties, where the insect held its own most successfully during those critical years—with a brief account of its progressive increase in numbers and extension of range from the year 1921 onwards.

178. Harrison, J. W. H. (1938). "*Plusia gamma* in the Isle of Muck in 1938." Entomologist, 71: 183.

This moth is a migrant species.

179. Fisher, K. (Grant, K.) (1938). "Migrations of the silver-Y moth (*Plusia gamma*) in Great Britain." J. Anim. Ecol. 7: 230–47.

This moth appears to be a migrant from the Continent, analogous to swallows and many other birds. Information collected by the author and received from the Insect Immigration Committee shows that this moth arrives in summer, breeds, and migrates south in the autumn. Maps and charts of seasonal distribution and migration are shown. The direction is often across or against the wind.

180. Grant, K. J. (1937). "Some recent migrations of the silver Y moth." S. East Nat. 42: 99–106.

A short discussion on the types of British migrant Lepidoptera. A short summary of records made, from 1932 to 1936, of the migrations of *Plusia gamma*, the silver-Y moth. The effects of wind. In about sixty records of migratory flights there is a slight preponderance of flights against the wind over flights with it. The improbability of *Plusia gamma* surviving the winter in England.

181. Goodall, C. J. (1938). "*Euphrydryas aurinea* in Herts." Entomologist, 71: 162.

A further instance of a single specimen of this local butterfly being found at a considerable distance from the nearest known colony.

182. Morley, A. M. (1938). "*Aplasta ononaria* at Folkestone." Entomologist, 71: 145–7.

Eight specimens, probably all descendants of a single female immigrant moth, were taken. All previous records of its occurrence in this country are listed. Further reference in **E. A. Cockayne** (1938). Entomologist, 71: 169–73.

183. Shrubsole, G. (1937). "Mollusca of the sheep ponds on the Eastbourne Downs." J. Conch. 20: 308–10.

A discussion on the method of colonization of artificial ponds near Eastbourne by Molluscs. The author attributes their presence to human agency.

8. REPORTS OF ORGANIZATIONS

184. Committee on Bird Sanctuaries in Royal Parks (England) (1938). "Report for 1937." (London: H.M. Stationery Office. Price 6*d*.)

Contains chiefly records, but some interesting, though scrappy, data on fluctuations of winter gull and water fowl populations.

185. Fisheries—England and Wales. Minist. Agric. Fish. (1937). "Salmon and freshwater fisheries: Report for the year 1936." Pp. 1–53. (London: H.M. Stationery Office. Price 1*s*.)

A graph shows annual fluctuations since 1909 in catch of salmon and migratory trout from 14 districts. There is a general similarity of trend. Abundant rainfall and an increase in efficiency of sewage disposal reduced the effects of pollution. Research was carried out on pollution by cyanide and tar acids in the Tyne, lead in a Welsh river, road dressings and milk wastes; on biological indicators of pollution; on the growth of brown trout and their eggs in soft waters.

186. Anon. [1937]. "Saorstát Éireann [Irish Free State] Report on the sea and inland fisheries for the year 1936." Pp. 1–32. (Government Publications Sale Office, 5 Nassau St., Dublin, C. 2. Price 9*d*.)

Eighteen appendices with short discussion. The Department examined samples of herring (young herring have become very scarce off the Donegal coast), carried out a salmon marking scheme and a study of the food and growth of brown trout in acid and alkaline waters.

187. Éire, Dep. Agric., Fish. Branch [1938]. "Report on the sea and inland fisheries for the year 1937." Pp. 1–35. (Government Publications Sale Office, 3–4 College St., Dublin. Price 9*d*.)

Statistics of catches and prices of marine and inland fisheries. Sea fisheries include demersal fishes (not separated into species), herring and mackerel and shellfish. Inland fisheries include salmon, trout and eels. Brief non-technical accounts of investigations into the biology of the herring, plankton and hydrography, salmon and trout are given with a summary of legislative measures.

188. Dove Marine Laboratory, Cullercoats, Northumberland (1938). Report for the year ending 31 July 1937. Third series, No. 5, 42 pp. (Marine Laboratory Committee of King's College, Newcastle upon Tyne. Price 5*s*.)

Includes a report of herring investigations and notes on fish living and breeding in the aquarium. A separate paper on conditioned responses in fishes is noticed elsewhere. (No. **70**.)

BRITISH ECOLOGICAL SOCIETY

ANNUAL MEETING AT UNIVERSITY COLLEGE, LONDON

5—6 January 1939

Soirée in the Department of Botany

On the evening of Friday, 5 January, about 80 members and guests were entertained at a soirée in the Department of Botany, University College, London.

An interesting series of exhibits was shown. Dr F. W. Jane showed a large number of very beautiful drawings and microscopic preparations of a large number of little known British flagellates. Many species of flagellates appear to be rare because not looked for at all, or at the wrong time of the year. Included in the exhibit were many hitherto undescribed species and even genera. A rough classification of habitats was suggested, and the habitat was shown for each of the species. Other exhibits showed the appearance of "annual rings" in sections of the fossil *Lyginopteris*, and vivipary in the fruiting heads of *Dipsacus vulgaris*.

Prof. Salisbury exhibited a series of full-scale drawings of the root systems of dune plants excavated by blowing away of sand. They included *Calluna vulgaris*, *Lotus corniculatus* (80 cm.), *Euphorbia portlandica*, *E. paralias* (130 cm.), *Hypochaeris radicata* (60 cm.) and *H. glabra* (60 cm.), *Ononis arvensis* (150 cm.), *Galium verum* (150 cm.), *Diplotaxis tenuifolia* (70 cm.), *Salvia verbenaca* and *Eryngium maritimum* (155 cm.).

At 9 p.m., Sir Arthur Hill gave an interesting talk on "The Art of living upside-down". He described the reaction of flowers to suspension in inverted positions, and illustrated the resultant types of movement by a large series of specimens, photographs and drawings. He pointed out also the interest of the natural inversion of leaves of *Alstroemeria* and *Bomarea* and of the positions taken up by the pitchers of Nepenthes.

The Annual Meeting

The twenty-fifth annual meeting of the Society was held in the Department of Botany, University College, London, on the following morning, Friday, 6 January, at 10 a.m., the President, Prof. A. G. Tansley, occupying the chair.

Prof. Tansley explained how pressure of work had made him unable to prepare a presidential address, and how the Council had made arrangements for it to be read at a meeting at Easter.

The minutes of the previous meeting were read and confirmed. The resignation of Mrs Hands was accepted and Mr Elflyn Hughes was elected to the membership of the Society. The report of the Hon. Secretary was then read and adopted.

Hon. Secretary's Report for the year 1938

The twenty-fourth annual meeting of the Society was held in the Botany School, Cambridge, on 6 January. On the evening of Friday, 5 January, between 80 and 100 members and guests were entertained at a soirée in the department where a large series of exhibits had been set out.

The Annual Meeting was held on the 6th, and after the business meeting seven very interesting papers were read to the Society. On the following morning a party of 30 under the leadership of Dr Godwin and Mr Tidmarsh, made an excursion by bus through the south-eastern fens and the Breckland margin. The sincere thanks of the Society are due to Prof. Brooks for having given us the generous hospitality of his department.

A new departure in the arrangements of the Society was the holding of an additional

meeting on 20 April in the Botany Department of Bedford College, London, to discuss problems of soil toxicity in Dorset heathland. After introductory accounts by Prof. Neilson-Jones and Dr Rayner, a long and interesting discussion followed, in which several distinguished guests spoke of the problems in relation to their own fields of forestry and soil science. After lunch there followed the inspection of a long series of exhibits illustrating different aspects of the problem. We are greatly indebted to Prof. and Mrs Neilson Jones and their assistants for an extremely profitable meeting.

The Summer Meeting of the Society was held in the University College of Wales, Aberystwyth, from 16 to 21 July. Several expeditions of very great interest were made to Tregaron Bog, to the Dovey dunes and salt marshes, to the Welsh Plant Breeding Station and to the field experiments in the Welsh mountains. A soirée was held on the evening of 16 July and evening meetings were held on the 19th and 20th. About 30 members attended the meeting and a number of these remained after the 21st and were conducted on further local ecological excursions. The Society has seldom had so successful a Summer Meeting and must be extremely grateful to Profs. Newton, Laurie and Stapledon, and their staffs for contributing so wholeheartedly and successfully to it.

In the past year two numbers of volume seven of the *Journal of Animal Ecology* have been published, appearing respectively in May and November; they contain respectively 198 and 226 pages. Twenty-eight original papers were published with 14 plates, in addition to notices and reviews. Notices of publications on Animal Ecology in this volume totalled 288.

Since the last annual meeting there have been issued two numbers of the *Journal of Ecology*, appearing in February and August, and containing respectively 254 and 247 pages with 7 plates. In this volume have been published 26 original papers, as well as notes and book reviews.

The Society's transplant experiments at Potterne are continuing satisfactorily in the hands of Mr Marsden Jones and Dr Turrill, and accounts of them occur in the current issue of the *Journal of Ecology*.

Since the last annual meeting the membership of the Society has risen from 350 to 363 members. 12 members have resigned or have died, and 25 new members have been elected. Of the present membership list 193 members received the *Journal of Ecology* alone, 116 the *Journal of Animal Ecology* alone, 52 received both *Journals* and one neither.

During the year the Society has suffered the loss by death of several valuable members, among them Mr B. D. Burtt and Mr C. F. M. Swynnerton, killed during air reconnaissance in East Africa, Prof. A. E. Boycott, F.R.S., and Prof. J. W. Bews, both men of the highest rank in our science. Prof. Boycott had been president of the Society in 1932 and 1933.

We are glad to note in the New Year's Honour's List the name of Sir R. G. Stapledon, an ecologist in practice and agriculturist in profession.

This year marks the end of the very long and devoted service of Mr Boyd Watt as Hon. Treasurer to the Society. We offer him our deep thanks for his able handling of our affairs and give him our sincerest good wishes.

The Hon. Treasurer made a provisional statement on the financial position of the Society, reporting a considerable positive balance on the year's working (see statement on p. 249). It was proposed from the chair and accepted *nem. con.* that Messrs William Norman and Son be reappointed auditors of the Society for 1939. Similar approval was given for grants of £5 to the Society's transplant experiments and of £10 to the Freshwater Biological Association.

The President then explained to the meeting that in view of Mr Boyd Watt's twenty-five years devoted service to the Society, the Council had nominated him on retirement from his post as Hon. Treasurer for Hon. Life Membership of the Society. This was carried with acclamation.

The alterations of rules proposed by the Council, to give effect to their wish that there should be two Hon. Treasurers and two Hon. Secretaries, were explained by the President and Hon. Secretary and were agreed *nem. con.* (for rules so approved see p. 251).

The meeting then proceeded to the election of officers and council members as follows:

Vice-President: Mr C. Diver (Dr Turrill retiring).
Hon. Treasurers: Dr A. S. Watt and Mr V. S. Summerhayes.
Hon. Secretaries: Dr H. Godwin and Dr G. C. Varley.
Ordinary Council Member: Dr O. W. Richards (Dr Ashby retiring).

The President then mentioned the arrangements for the Easter Meeting, which by the kindness of Prof. William Brown would be held in Imperial College, South Kensington. He mentioned the possible alternatives of the New Forest or Plymouth for the Summer Meeting, and outlined a scheme for a National Atlas, in the preparation of which the Society had been asked to co-operate. The Hon. Secretary briefly indicated the steps which the Council had taken to co-operate with the Forestry Commission in initiating a scheme for Ecological reserves in different parts of the country.

Mr Richard Freeman, Magdalen College, Oxford, was elected a member of the Society.

The President read a letter from Mr Dudley Stamp suggesting the possibility of having a mechanism for life membership of the Society instead of the payment of annual subscriptions: it was agreed to refer the matter to the Council.

At 11.10 a.m., the President opened the symposium on the Reciprocal Relationship of Ecology and Taxonomy. An account of the proceedings will be found in the *Journal of Ecology*. Those who spoke were:

The President	Dr J. Burtt Davy	Mr R. Ross
Prof. E. J. Salisbury	Mr A. J. Wilmott	Mr H. Baker
Dr O. W. Richards	Dr B. P. Uvarov	Dr H. Godwin
Dr J. Huxley, F.R.S.	Dr A. R. Clapham	Dr A. S. Watt
Dr D. H. Valentine	Mr C. B. Williams	Mr F. T. K. Pentelow
Capt. C. Diver	Mr C. S. Elton	Dr W. B. Turrill
Mr V. S. Summerhayes		

The discussion continued through the afternoon. In adjourning the meeting the President gave very hearty thanks to Profs. Salisbury and Hill for their hospitality, and to Prof. Salisbury and Dr Barbara Russell-Wells for the trouble they had taken in organizing the soirée and the meeting. The meeting closed at 4 p.m. with tea generously provided by Prof. Salisbury.

EASTER MEETING, 1938

A special meeting of the Society was held in the Botany Department, Bedford College, London, at 11 a.m., on 20 April 1938, the President, Prof. A. G. Tansley, in the chair. Several distinguished guests were present by invitation, Dr Crowther, Dr Jacks, Dr Lewis, Dr Guillebaud and Sir Albert Howard.

An informal account was given by Prof. Neilson Jones of some of the characteristics, including that of apparent toxicity, associated with the soils of Wareham Heath. He described the poor growth of conifers in this soil and showed that *Nicotania* seedlings grown in pots of it only thrive at the margins. He showed that steaming the soil mitigated the effect, and that the vapour from steamed soils produced epinastic movements in tomato like those produced by ethylene. In a film of nutrient agar poured over the soil, fungal spores germinate but the hyphae do not grow: steaming and other pre-treatments remove this effect. The condition of "fused needle" in *Pinus contorta* and *P. insignis* was described and it was said that no pathogen had been detected.

This was followed by a general description, given by Dr M. C. Rayner, of research work done at Wareham since 1932, with special reference to forestry experiments. She showed that seedlings on the sterile soil had no tertiary roots and no mycorrhiza, and demonstrated that good growth and good mycelium go together. The beneficial effects of the addition of composts of straw, hops, sawdust and *Molinia* to the soils were described, and illustrated by very striking photographs.

An extremely interesting and controversial discussion followed, in which many members and guests took part.

After lunch the meeting examined a long series of exhibits dealing with the same problems, and discussed the exhibits with the individual research workers who had produced them.

The discussion was resumed at 3.30 p.m., and some time later closed with a very delightful tea party given in the College. Prof. Tansley expressed the grateful thanks of the Society for the generous hospitality given us by Prof. and Mrs Neilson Jones, their research workers, and the College authorities.

SUMMER MEETING AT ABERYSTWYTH

16—21 July 1938

At the kind invitation of Profs. Newton, Laurie and Stapledon, the Summer Meeting of the Society was held at Aberystwyth. The meeting opened with a soirée held in the University College of Wales, at 8.15 p.m. A large number of interesting exhibits had been set out, and during the evening songs were given by some of the University students.

Sunday, 17 *July*. A visit was paid to Tregaron Bog under the leadership of Dr Godwin. The large west bog is a typical atlantic raised-bog (Hochmoor) with a well developed rand beside the river Teifi, and remains of a lagg where the bog meets the hillside. The highest part of the bog is occupied by very characteristic regeneration complex in which pools and *Sphagnum* hummocks alternate.

Monday, 18 *July*. The meeting visited the gardens of the Welsh Plant Breeding Station, where Dr Jenkin demonstrated the basis of production of seed for pasturing. He emphasized the need for selection for permanence, leafiness and vigour. He stressed the extremely heterozygous nature of the material and its great phenotypic variation. In the greenhouse Dr Jenkin described the genetical work on *Lolium* and demonstrated the practical methods of performing crosses. He then showed the party the results of some extremely interesting interspecific and intergeneric crosses, drawing especial attention to the doubtful origin of *Festuca loliacea*. This is supposed to be a cross between *F. pratense* and *Lolium perenne* but indistinguishable plants can be produced in other ways. The party went on to the experiments in the Penglais fields, in which were growing rows of clones of many selected and commercial strains of Timothy and other grasses. The close leafy habit of types selected from old pastures contrasted strongly with the stemmy open growth of the commercial strains. The testing for late flowering and resistance to rust were also demonstrated.

Following an improvement in the weather the party travelled in the afternoon to visit the Cahn Hill Improvement Scheme. All the hill-pasture experiments were concerned more or less with the influence of the biotic factor on sward development. Many remarkable effects were shown of treatment by phosphates or basic slag, with or without the introduction of new species such as wild white clover and Yorkshire fog. There was a very marked effect of the transport of minerals with "stock nitrogen" from the lower manured slopes to higher pastures. In particular the effects of night camping by cattle in sheltered hollows at high altitudes, was very strongly marked, such areas showing a great increase in *Agrostis* and establishment of clover.

In the evening at 8 p.m., there was a small exhibit staged in the Botany Department of University College, of various aspects of the work of the Plant Breeding Station, and different members of the staff gave short talks on genetical and ecological aspects of their

work. Dr Jenkin gave an account of genetics in relation to ecology, drawing examples from his very wide experience of the grasses. A point of particular interest was the occurrence of two types of *Arrhenatherum elatius*. The extreme bulbous type is found in arable land, and most hedgerow or wayside plants are intermediate in type. Completely non-bulbous plants have to remain winter green. The *F*1 crosses between the extreme types are intermediate. Mr R. D. Williams described his work on genotypes of red clover. The plants are diploid (2×7) and normally cross-fertilized with very common self-sterility. He showed specimens illustrating the determinance of several features such as pubescence, dwarfness, sterility and chlorophyll-deficiency. Marked linkage groups have been demonstrated. Mr W. Davies gave a short description of the grasslands of Wales, and stressed the fact that altitude and geology are not the only factors determining grassland type. He suggested that the dominance of *Agrostis* is largely due to grazing. Prof. Stapledon concluded the series by some general remarks on the ecology of Welsh pastures, again pointing out the great importance of grazing treatment.

Tuesday, 19 *July*. The party visited Llety-evan-hen to see the experiments of the Welsh Plant Breeding Station on controlled grazing and manuring upon native *Molinia* and *Fescue-Agrostis* swards. The cages under different manurial treatment and strictly controlled grazing showed extremely marked differences from one another, although only begun in 1930. It was very marked that new species made their appearance wherever suitable conditions were created, although no seeds were sown, and although samples showed no buried viable seeds. Within two years the controlled grazing and manuring changed the former *Molinia-Nardus* sward to *Fescue-Agrostis*. After lunch at the Plant Breeding Station the party was shown experiments on grazing and manuring in a valley marsh, where changes as striking as those on the upland pastures were evident. Across one set of plots there was an extremely marked low-fertility strip on the site of a former hedgerow.

At 8 p.m. in the Department, the following series of short papers were given:

"Distribution of hill bogs in Cardiganshire": J. B. Jones.
"Soil Fauna of the Dovey Estuary": Dr Watkin.
"Preliminary account of Blaen Brefi bog (1300 ft.)": E. G. Davies.
"Observations on *Rhynchospora alba*": E. M. Canton.
"Tregaron Bog": H. Godwin.

Wednesday, 20 *July*. The party visited the sand dunes at Ynyslas under the leadership of Mr E. H. Chater. The dunes showed very marked effects of wind erosion and rearrangement, and extensive dune lows and sandy marshes. The effect of blowing sand in promoting the flowering of *Psamma* was very well seen. After lunch the party visited the salt marshes on the shores of the Dovey Estuary, and were shown the evolution of different types of pans from channels and depressions to their final disappearance into close sward. It was quite clear that several different levels of marsh were represented, and distinct phases of erosion and deposition following changes in the course of the Dovey currents.

In the evening there was an exhibition in the Department of Zoology of work on Animal Ecology and the following papers were read:

"Faunistic history of River Rheidol in relation to lead pollution": Dr K. E. Carpenter.
"Remarks on effect of pollution on plants": Prof. Newton.
"The effect of calcium on the toxicity of heavy metal salts to fish": Dr J. R. E. Jones.

At the conclusion of the meeting Prof. Tansley expressed our deep gratitude to our hosts for providing such an exceptionally interesting and satisfactory meeting. He expressed particular thanks to Profs. Newton, Laurie, and Stapledon and the stewards, Mr J. B. Jones and Mr E. G. Davies who had so successfully organized the excursions.

Several members prolonged their stay beyond the official end of the meeting, and were taken on further ecological excursions into the woodland and mountain pastures of the district.

BRITISH ECOLOGICAL SOCIETY

REVENUE ACCOUNT FOR THE YEAR ENDING 31 DECEMBER 1938

Income

	£ s. d.	£ s. d.
Subscriptions received, including arrears, and *less* Payments in advance		475 18 0
Interest on Investments	39 15 0	
Interest on Deposit Account	1 5 0	
		41 0 0
Index volume to *Journal of Ecology*, vols. I–XX:		
Sales	15 18 0	
Expenses	3 7 4	
		12 10 8
		£529 8 8
Journal of Ecology, 1938:		
Sales: Current vol. XXVI, 1938		559 0 0
Back volumes and parts		41 6 8
Reprints of papers		67 2 0
Grant: Received per Editor		10 0 0
		677 8 8
Balance (see above, under Expenditure)		45 11 2
		£722 19 10
Journal of Animal Ecology, 1938:		
Sales: Current vol. VII, 1938		250 18 8
Back volumes and parts		95 5 2
Reprints of papers		54 17 0
		401 0 10
Grant: From Bureau of Animal Population, Oxford ...		5 0 0
		406 0 10
Balance (see above, under Expenditure)		236 0 10
		£642 1 8

Expenditure

	£ s. d.	£ s. d.
Working Expenses:		
Printing, Stationery, etc.	5 5 6	
Postages and Travelling	13 13 5	
Bank Charges	1 3 3	
Clerical assistance	15 0 0	
Meetings, Soirée, etc.	2 4 0	
Audit	3 3 0	
		40 9 2
Grants:		
Fresh Water Biological Association	10 0 0	
Transplants Experiments Fund	5 0 0	
		15 0 0
Journal of Ecology. Cost *less* Sales		45 11 2
Journal of Animal Ecology. Cost *less* Sales		236 0 10
		337 1 2
Balance: Surplus for the Year, carried forward ...		192 7 6
		£529 8 8
Journal of Ecology, 1938:		
Cost: Paper, Blocks, Printing and Binding		599 4 7
Publishers and Commission		84 9 8
Carriage and Postages		35 5 7
Insurances		4 0 0
		£722 19 10
Journal of Animal Ecology, 1938:		
Cost: Paper, Blocks, Printing and Binding		550 19 10
Publishers' Commission		51 2 5
Carriage and Postages		20 13 11
Insurance		6 16 3
Sundries		2 9 3
Bureau of Animal Population, Oxford, for special services		10 0 0
		£642 1 8

BALANCE SHEET AT 31 DECEMBER 1938

Liabilities

	£ s. d.	£ s. d.
Subscriptions prepaid for 1939/31		18 9 0
Library Fund		1 5 0
General Revenue Account, Surplus in hand:		
Balance at 31 December 1937	1087 11 3	
Surplus for the Year 1938	192 7 6	
		1279 18 9
		£1299 12 9

Assets

	£ s. d.	£ s. d.
Cash in Hand at Westminster Bank:		
Current Account	27 11 11	
On Deposit	200 0 0	
		227 11 11
Investments at Cost:		
Brought forward, 31 December 1937	915 13 0	
Bought February 1938, £150 of 3½ % War Loan ...	156 7 10	
		1072 0 10
		£1299 12 9

Totals held, 31 December 1938:	£ s. d.
£850 of 3½ % War Loan at cost ...	873 10 10
£200 of 5 % Conversion Loan ...	198 10 0
	£1072 0 10

NOTE A. The market value of the above Investments at 31 December 1938:

3½ % War Loan at 98	£833
5 % Conversion Loan 109½	£219
	£1052

NOTE B. A further Asset not valued above is the unsold Stock of Journals and Index Volumes held by the Publishers for the Society.

(Signed) HUGH BOYD WATT,
Hon. Treasurer.

Audited and found correct and as shown by the Account Books of the Society. The Bank Balances have been verified by Bank Certificates, and also the Investments.

(Signed) WM NORMAN & SONS.
Chartered Accountants.

120, BISHOPSGATE, LONDON, E.C. 2.

1 *February* 1939

THE BRITISH ECOLOGICAL SOCIETY

FOUNDED 1913

CONSTITUTION AND RULES

1. The object of the BRITISH ECOLOGICAL SOCIETY shall be to promote and foster the study of Ecology in its widest sense.

2. The Society shall consist of Ordinary Members, Hon. Members and Associates as defined in these rules.

3. Applicants for Membership of the Society shall be proposed by one Member (from personal knowledge) or by an Officer of the Society (not necessarily with personal knowledge) and seconded by one or more other Members. Such applications shall be made on a form to be supplied by the Hon. Secretaries, and duly filled up and signed by the applicant.

Election shall take place either at a General Meeting or at other times by resolution of the Council. A majority of votes in favour shall result in the election of the applicant.

The Secretaries may, however, be empowered by the Council to circulate the names of applicants for membership to members of Council by post, and if they receive no intimation of objection within one week, the applicant shall be deemed to be elected.

4. Subscriptions shall be payable in advance and shall be due on January 1st each year. The minimum Annual Subscription for Ordinary Membership shall be twenty-five shillings (25*s.*) and for Associate Membership seven shillings and sixpence (7*s.* 6*d.*). Members who pay a yearly subscription of 25*s.* shall have the right to receive post free **either** *The Journal of Ecology* **or** *The Journal of Animal Ecology*. An Annual Subscription of 45*s.* shall entitle Members to receive post free **both** of the Journals above named.

5. In addition to receiving one or both of the Journals of the Society, ordinary members shall have the following privileges:

(*a*) To receive on application any other publications of the Society free or at a reduced rate, as the Council may from time to time determine.

(*b*) To have the use on loan, under regulations, of any photographs or lantern slides in the Society's collections, and of books, maps and pamphlets in the Society's Library.

(*c*) To vote in the election of Council and of Officers.

(*d*) To be eligible for service on the Council and its Committees, or as Officers.

6. Associate Members shall have the right to attend Meetings and Excursions, to obtain through the Secretaries such advice and assistance as the Society can afford, to have the use of photographs and the Library, but they shall not have the privileges of Ordinary Members indicated in 5 (*c*) and 5 (*d*).

7. Local Natural History Societies may at the discretion of the Council be allowed to subscribe to the Society not less than twenty-five shillings (25*s.*) per annum and shall thereby be entitled to receive a copy of **either** of the two Journals of the Society, or on payment of forty-five shillings (45*s.*) per annum, to receive **both** Journals of the Society. In either case they shall also be entitled (*a*) to such advice or assistance as the Society can afford, and (*b*) to send two delegates to the Society's Meetings, to have the same privileges as Associate Members as regards such Meetings.

8. The Society shall be governed by a Council of not less than fifteen, and not more than twenty Members consisting of the Officers of the Society, namely, the President, two Vice-Presidents, the two Hon. Editors, the two Hon. Secretaries and the two Hon. Treasurers, with ordinary members of Council.

Officers and ordinary members of Council shall be elected at the Annual Meeting of the Society.

9. Each ordinary member of Council shall be elected for a period of four years, at the end of which time he shall retire. He shall not be eligible for re-election until the Annual Meeting of the year following that of his retirement.

An ordinary member of Council when elected an Officer of the Society shall cease to be an ordinary Council member: on expiry of office the retiring President, Hon. Secretaries, Hon. Treasurers and Hon. Editors shall be eligible for immediate re-election as ordinary members of Council, and the retiring Vice-President shall complete his term of four years' service on the Council.

10. The President and the two Vice-Presidents shall be nominated from among the members of Council. The two Hon. Editors and the two Hon. Secretaries shall retire at the end of each year but shall be eligible for immediate re-election.

11. The President of the Society shall hold office for two years, and it shall be his duty to deliver an address to the Society at the Annual Meeting next after that at which he was elected.

12. One Vice-President shall be appointed each year and shall hold office for two years.

13. The two Hon. Treasurers shall hold office for three years and shall be eligible for re-election. The Hon. Treasurers shall keep the Society's funds and shall be responsible for collection of subscriptions. Their sanction shall be required for the disbursement of the Society's moneys and they shall present a financial statement at the Annual Meeting. The financial status and policy of the Society shall be considered each year at a meeting of the Council held as soon as practicable after the audit. The audited accounts shall be published in the Journals of the Society.

14. If any Council member does not attend at least one meeting of the Council during the year he shall retire at the end of the year, but shall be eligible for re-election.

15. At least one fortnight before the Annual Meeting the Secretaries shall circulate to all Members of the Society a list of the members of Council including Officers, indicating those who retire and adding the names of nominees of the Council to fill the vacancies.

16. Members may propose for ballot at the Annual Meeting the name or names of any duly qualified Member or Members in place of any or all of the Council's nominees.

17. The Council shall have power to co-opt any ordinary Member of the Society to fill vacancies occurring during the year among Council or Officers, the tenure of such co-opted Members to terminate at the next Annual Meeting.

18. At the Annual Meeting, after nomination by the Council, persons who have rendered conspicuous service to the subject of Ecology may be elected Honorary Members of the Society.

Such Hon. Members shall receive free either or both Journals of the Society as the Council may determine, and shall also have the other privileges of ordinary Members of the Society.

19. The Annual Meeting shall be held in December or in the following January. At least one other Meeting shall be held later in the year. Further Meetings and Excursions may be held at such times and places as the Council may from time to time determine.

20. At the Annual Meeting the Members of the Society present shall ballot for Officers and Council and consider any other business brought before them by the Council or by any Member, of which four weeks' notice in writing has been given to the Secretaries.

21. Alterations of the Rules shall only be made at the Annual Meeting and require six weeks' notice in writing to the Secretaries and a majority of two-thirds of the Members voting.

22. Members desiring to present communications at any Meeting must give due notice to the Secretaries, stating the nature of the communication and the time required.

23. At any Meeting of the Society the Chairman shall decide as to procedure and the order of business. It shall be within the Chairman's discretion to admit communications or other business, other than alterations to the Rules, not included in the programme.

24. A Meeting of the Council to consider the Annual Report shall be held shortly before the Annual Meeting.

25. The Society shall issue two Journals, *The Journal of Ecology*, and *The Journal of Animal Ecology*.

26. The subscription price of each Journal to others than Members of the Society shall be as determined by the Council.

27. No Member shall be entitled to receive the Journals of the Society whilst his subscription is in arrear.

(This revised formulation of the constitution and rules was accepted at the Annual Meeting of the Society, 6 January 1939.)

LIST OF MEMBERS (16 JANUARY 1939)

E. = Takes *The Journal of Ecology*. A. = Takes *The Journal of Animal Ecology*.

Corrections, omissions or changes of address should be notified at once to the *Hon. Secretary*, DR H. GODWIN, Botany School, Cambridge.

E. A. **Adams**, Dr Charles C.; New York State Museum, Albany, N.Y., U.S.A.
E. **Adamson**, Prof. R. S., M.A.; The University, Cape Town, S. Africa.
A. **Alexander**, W. B., M.A.; University Museum, Oxford.
A. **Allee**, W. C.; Zoology Building, University of Chicago, Chicago, Ill., U.S.A.
A. **Allen**, E. F., B.A., M.B.O.U.; Dept. of Agriculture, Teluk Anson, Perak, Malaya.
E. **Allorge**, Pierre; Laboratoire de Cryptogamie, 63, Rue de Buffon, Paris.
E. **Alun-Roberts**, R.; Agricultural Dept., University College, Bangor.
E. **Anand**, P. L., M.Sc.; Dept. of Biology, Sanatana Dhanna College, Lahore, India.
E. **Andersonian Naturalists' Society** (cf. Glasgow).
E. A. **Arkwright**, J. A., M.D., F.R.S.; Lister Institute, Chelsea, London, S.W. 1.
E. **Armitage**, Miss E.; Dadnor, Ross, Herefordshire.
E. **Ashby**, Prof. Eric, B.Sc.; The University, Sydney, N.S.W.
E. **Bacon**, Mrs Alice; The Technical College, Brighton.
E. **Baker**, H.; University Dept. of Botany, High St., Oxford.
A. **Barber**, Miss E. G.; Harborne, Westbourne Avenue, Emsworth, Hants.
E. **Barnes**, Dr B.; 28, Torridon Road, London, S.E. 6.
A. **Barnes**, H. F., Ph.D.; Rothamsted Experimental Station, Harpenden, Herts.
E. **Bates**, G. H., B.Sc.; The Farm Institute, Penkridge, Stafford.
E. A. **Beauchamp**, R. S. A., B.A.; Connellmore, Cheltenham, Glos.
E. **Bell**, Prof. H. P.; Dalhousie University, Halifax, Nova Scotia.
A. **Bertram**, G. C. L., M.A.; St John's College, Cambridge.
E. **Bhâradwâja**, Prof. Y.; Dept. of Botany, Hindu University, Benares, India.
E. **Bharucha**, Dr F. R.; 6, Alexandra Road, New Gamdevi, Bombay 7.
E. **Blackburn**, K. B., D.Sc.; Armstrong College, Newcastle-upon-Tyne.
E. **Blackman**, G. E.; Wick Cottage, Westleigh Av., Putney Hill, London, S.W. 15.
E. **Bloomer**, H. H.; Longdown, Sunnydale Road, Swanage, Dorset.
E. **Bor**, N. L., M.A., D.Sc.; Forest Research Institute, New Forest P.O., Dehra Dun, U.P. India.
E. **Børgesen**, Dr F. C. E.; Botanisk Museum, Gothersgade 130, Copenhagen.
A. **Bosanquet**, S. J. A.; Fisheries' Laboratory, Lowestoft, Suffolk.
A. **Boyd**, A. W., M.C., M.A.; Frandley House, nr Northwich, Cheshire.
E. **Boyd**, L.; Royal Botanic Gardens, Edinburgh.
E. **Bracher**, Miss Rose, Ph.D.; Dept. of Botany, The University, Bristol.
E. **Braid**, Major K. W.; 6, Blythswood Square, Glasgow.
E. **Braun**, Miss E. L.; 2702, May Street, Cincinnati, Ohio, U.S.A.
E. **Brenchley**, Dr Winifred E.; Rothamsted Experimental Station, Harpenden, Herts.
A. **Brindley**, Mrs M. D.; 25, Madingley Road, Cambridge.
E. **Brodsky**, Prof. A.; Middle Asiatic State University, Tashkent, Usbekistan, U.S.S.R.
E. **Brooks**, Prof. F. T., M.A., F.R.S.; Botany School, Cambridge.
A. **Brown**, F. M.; Bryancliffe, Hungerford Road, Huddersfield, Yorks.
E. **Burges**, N. A.; Botany School, Cambridge.

E. A. **Burtt**, B. L.; The Herbarium, Royal Botanic Gardens, Kew, Surrey.
E. **Burtt Davy**, Dr J.; Shotover Furze, The Ridings, Headington, Oxford.
E. **Butcher**, R. W., B.Sc.; Fisheries Research Station, Alresford, Hants.
A. **Buxton**, Prof. P. A.; London School of Hygiene, Keppel Street, London, W.C. 1.
E. **de Caen**, Mrs, Ph.D,; Springfield, Dalgany, Co. Wicklow, Ireland.
A. **Cameron**, A. E., D.Sc.; Dept. of Entomology, 10, George Square, Edinburgh.
A. **Carey**, Miss E., Foxhill, Bracknell, Berks.
A. **Carpenter**, Prof. G. D. Hale, M.B.E., D.M.; Penguelle, Hid's Copse Road, Cumnor Hill, Oxford.
A. **Carpenter**, J. R., M.Sc.; 2670, N. Alpine Road, Grand Rapids, Michigan, U.S.A.
A. **Carpenter**, Prof. K. E., Ph.D.; Zoology Dept., University of Liverpool.
A. **Carter**, Dr G. S.; Corpus Christi College, Cambridge.
E. **Carter**, Dr Nellie; Armeria, Petersham Road, Richmond, Surrey.
A. **Cawkell**, E. M., 10, Algier's Road, Ladywell, London, S.E. 13.
E. **Chapman**, P. C.; Charterhouse School, Godalming, Surrey.
A. **Chapman**, Prof. R. N.; University of Hawaii, Honolulu, Hawaii.
E. **Chapman**, V, J.; 13, Brookside, Cambridge.
A. **Charteris**, Hon. Guy; 24, Oxford Square, London, W. 2.
A. **Chitty**, D. H.; Bureau of Animal Population, University Museum, Oxford.
E. **Clapham**, Dr A. R.; Botanical Dept., The University, Oxford.
E. A. **Clements**, Prof. F. E.; Mission Canyon, Santa Barbara, California.
A. **Colquhoun**, M. K.; Lane's End House, Woodlands St Mary, Newbury, Bucks.
E. **Conway**, Miss V. M.; 61, De Freville Avenue, Cambridge.
E. **Cooper**, Prof. W. S.; Dept. of Botany, University of Minnesota, Minneapolis, Minn.
E. **Cotton**, A. D.; The Herbarium, Royal Botanic Gardens, Kew, Surrey.
A. **Corley**, H. V.; Hyron's Lodge, Amersham, Bucks.
E. **Cowles**, Prof. H. C.; University of Chicago, Chicago, Ill., U.S.A. (*Hon. Life Member*).
E. **Croydon Natural History and Scientific Society**, 27, High Street, Croydon.
E. **Curtis**, Miss W. M., B.Sc.; 381, Holly Lodge Mansions, Highgate, London, N. 6.
A. **Dalgety**, C. T.; Denver Hall, Downham Market, Norfolk.
A. **Darling**, F. F., Ph.D.; Brae House, Dundonnell, by Garve, Wester Ross, Scotland.
E. **Davey**, Miss A. J., M.Sc.; University College of N. Wales, Bangor, N. Wales.
E. **Davies**, W. C.; The Cawthron Institute, Nelson, N.Z.
E. A. **Davis**, D. H. S.; Dept. of Public Health, Pretoria, S. Africa.
E. **Davis**, T. A. W.; Forestry Station, Mozaruni, British Guiana.
E. **Dawson**, R. B., M.Sc., F.L.S.; St Ives Research Station, Bingley, Yorks.
E. **Delf**, Dr E. M.; Westfield College, Hampstead, London, N.W. 3.
A. **Diver**, C.; 40, Pembroke Square, Kensington, London, W. 8. (*Vice-President*).
A. **Donaldson**, R. P.; Royal Society for Protection of Birds, 82, Victoria Street, London, S.W. 1.
E. **Dowling**, Miss R. E., M.Sc.; The Nest, Ledgers Road, Slough, Bucks.
A. **Duncan**, A. B., B.A.; Gilchristland, Closeburn, Dumfries.
E. **Dundas**, J.; Chief Conservator of Forests, Ibadan, Nigeria.
E. **Du Rietz**, Prof. Einar; Vaxtbiologiska Institutionen, Upsala, Sweden.
E. A. **Dyke**, F. M., B.Sc.; Branksome, Boreham Woods, Herts.
E. **Edwards**, Miss D. A., 35, Queen's Gate Mews, Kensington, London, S.W. 7.
E. A. **Eggeling**, W. J., B.Sc.; Forest Office, Entebbe, Uganda.
E. **Ekblaw**, Dr W. E.; Clark University, Worcester, Mass., U.S.A.
A. **Ellis**, R.; 2420, Ridge Road, Berkeley, California, U.S.A.
E. A. **Elton**, Charles; Bureau of Animal Population, University Museum, Oxford (*Hon. Editor of the Journal of Animal Ecology*).

E. **Essex Field Club, The** (Essex Museum of Natural History, Romford Road, Stratford, Essex).
E. **Evans**, E. Price; White Broom, 69, Westgate, Hale, Cheshire.
A. **Evans**, F. C.; Oriel College, Oxford.
E. **Evans**, G. C.; Botany School, Cambridge.
A. **Eyre**, Miss J.; Dept. of Zoology, University of Cape Town, S.A.
E. **Falk**, P.; 24, Rokeby House, Rugby.
E. A. **Featherly**, Prof. H. I.; Oklahoma Agricultural and Mechanical College, Stillwater, Okla., U.S.A.
E. **Fenton**, E. Wyllie, D.Sc.; 13, George Square, Edinburgh.
A. **Fidler**, J. H.; Warrenside, Mapledurham, Reading.
E. **Fisher**, H. S., M.Sc.; 35, Alexandra Road, Pietermaritzburg, Natal.
A. **Fisher**, J. M. Mc.; Zoological Society of London, Regent's Park, N.W. 8.
E. A. **Fitzgerald**, D. V.; Clammer Hill, Haslemere, Surrey.
E. **Foggie**, A., B.Sc.; c/o Conservator of Forests, Forestry Department, Accra, Gold Coast, Africa.
A. **Ford**, J.; Tsetse Research Dept., Shinyanga, Tanganyika Territory.
E. **Fraser**, G. K., M.A., D.Sc.; Macaulay Institute, Craigiebuckler, Aberdeen.
A. **Freeman**, R.; Magdalen College, Oxford.
E. **Fritsch**, Prof. F. E., F.R.S.; Pilgrim's End, West Humble, Dorking.
E. **Fuller**, Prof. G. D.; Botany Dept., The University, Chicago, Ill., U.S.A.
E. **Galloway**, J. A.; Oak Bank, Bowness on Windermere, Westmorland.
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